Late Pleistocene and Holocene Paleolimnology and Climate History in Southern Sweden Reconstructed from Chironomid, Diatom and Pollen Records

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Chapter I

Introduction

The Pleistocene, commonly referred to as 'the Ice Age', is generally regarded as having drastic climate changes. The following 11,500 years, known as the Holocene, have long been perceived as a period of environmental stability (Roberts, 1998). Little change in climate, vegetation, fauna and edaphic conditions are thought to have occurred. Since the development and refinement of paleoenvironmental reconstruction methods, we have begun to understand that this view is too simple. The Holocene has, in Europe and in other regions of the world, been a succession of warmer and cooler periods, wetter and drier climate conditions, even though the amplitude of change was not as large as in glacial times. Detailed environmental reconstructions using biological indicators cannot only help to understand this past climate change, but also to validate and improve climate models inferring future climate trends (Smol et al., 1991) or give valuable information to improve ecosystem management (Smol, 1992; Walker, 1993).

Even though ecosystems and their components are controlled by a complex interaction of environmental factors, climate is one of the strongest abiotic determinants affecting aquatic ecosystems (Smol et al., 1991). Differentiation between the effects of climate warming and eutrophication may be difficult within aquatic species communities (Brodersen and Anderson, 2002). Because anthropogenic alteration of lake ecosystems in temperate regions may have occurred from prehistoric times and overrides the effects of natural variability, the majority of the climate reconstructions are derived from remote sediment records at sites in high-altitude and high-latitude regions. Quantitative reconstructions covering the whole Holocene in areas with a long history of human impact are still sparse.

Several different archives have been used to infer past climate and subsequent environmental change, including tree rings, ice cores, glacier movements, speleothems, and marine and lake sediments. In lake sediments, a variety of proxies have been used, including geological (mineral magnetism, particle size distribution, chemical composition) and biological (pollen, diatoms, chironomids, cladocera, chrysophyte cysts, plant macrofossils, stable isotopes from ostracod shells, algal pigments) compartments.

The most promising way to detect the effects in modern species distribution caused by e.g., anthropogenic disturbance, is a 'multiproxy' approach using several complementary indicators. Among the biological indicators for reconstructing paleoenvironmental change, chironomids (Insecta: Diptera: Nematocera: Chironomidae) and diatoms (Bacillariophyceae) have played an important role in the last decades. Transfer functions using modern species distribution data to infer past environments from fossil assemblages have been developed and successfully applied (e.g., Birks et al., 1990; Walker et al., 1991).

In Southern Sweden generally, and specifically Blekinge, the environmental change brought about by the end of the glacial

and the early Holocene are extremely well-documented. This includes e.g., patterns of deglaciation and sedimentation, coastline displacement and vegetation development (Berglund, 1964, 1966a,b; Björck, 1979; Ringberg, 1979; Björck, 1981; Liljegren, 1982; Ising, 2001; Lundqvist and Wohlfarth, 2001; Yu, 2003). The biological record contained within lake sediments and its potential as a complementary source of information for Quaternary environmental change still remains to be explored in this region. The effect of sea-level changes and land-lifting processes, leading to the isolation and re-connection of lake basins from the Baltic Sea and its predecessor, the Baltic Ice Lake, could be expected to have exerted significant impact on the biota of affected lakes, in addition to the general trends of environmental change during the Holocene, be it of natural or anthropogenic origin.

In this study, the late-glacial and Holocene sediment sequences of two adjacent lakes in Blekinge, Southern Sweden, were analysed for biological indicators. The objectives of this study were to reconstruct the individual paleoecological history of these lakes in a multi-proxy approach and to set their local development in relation to regional and global patterns of environmental and climate change within the late-glacial and the Holocene. Lake Stora Kroksjön is situated below the former highest coastline and its basin was once connected with the Baltic Ice Lake, while Lilla Torkelsjön is located immediately above the former highest coastline. Sediment properties, along with chironomids, diatoms and other biological remains were used to reconstruct paleoenvironmental conditions and changes. A mean July air–temperature transfer function from Norway (Brooks and Birks, 2000a, 2001) was applied to the fossil chironomid data to infer the summer temperature course during the last 14,000 years.

Specifically, the aims of this study were to:

1. document the late-glacial and post-glacial development of Lakes Stora Kroksjön and Lilla Torkelsjön in terms of their limnology, hydrology and ecology
2. obtain a quantitative temperature reconstruction at both sites
3. by comparison of both sites discern local effects from temperature and environmental trends acting on a higher spatial scale
4. validate the temperature reconstructions by placing them into relation with paleo-climate data from other independent archives
5. evaluate whether the connection to the Baltic Ice Lake has had an important impact on the limnology of Lake Stora Kroksjön

Chapter II

Paleoenvironmental reconstructions

1 Quantitative paleoenvironmental reconstructions

Many paleoecological studies aim to reconstruct specific features of past environments from fossil species assemblages preserved in lake, bog, or marine sediments. The value of an environmental variable (e.g., total phosphorus (TP) concentration) is expressed as a function of the biological data (e.g., diatom assemblages), which is thus used as a 'proxy' for the TP values. Quantitative environmental reconstructions are based on
a) modern calibration data sets (or 'training sets'), in which a bio-indicator of interest is sampled at a large number of sites in a biogeographical region along the environmental gradient of interest, while the environmental factors at each site are measured (Figure II.1, upper half), and
b) a fossil record of the indicator, preferably derived from the same biogeographical region (Figure II.1, lower half).

The fossil bio-indicators' species abundances are via a transfer function set into quantitative relation to the environmental variables governing the calibration data set. Thus, environmental variables can be expressed as a function of biological data. Some of the basic assumptions underlying quantitative environmental reconstructions (Birks, 1995) are:

- The taxa of the modern training set need to be systematically related to the environment in which they live.
- The environmental variable to be reconstructed is, or is linearly related to, an ecologically important determinant in the ecological system of interest.
- Other environmental variables than the one of interest have negligible influence, or their joint distribution with the environmental variable in the fossil set is the same as in the training set.
- Any inference model using modern data as calibration data sets to infer past environmental data assumes that the ecological response to the environmental variable, i.e. species optima and tolerances, have not changed over time.

There are two arguments for using the last assumption (principle of uniformitarianism) on late-glacial and Holocene environments: the short investigation period in terms of evolutionary relevant time spans (Bennett, 1997) and the fact that modern arctic and alpine species occur in similar environmental conditions as inferred for the late-glacial by independent proxies as e.g., δ^{18}O curves, palynological evidence etc.

Bio-indicators that can be used as meaningful proxies for environmental variables should have the following properties:

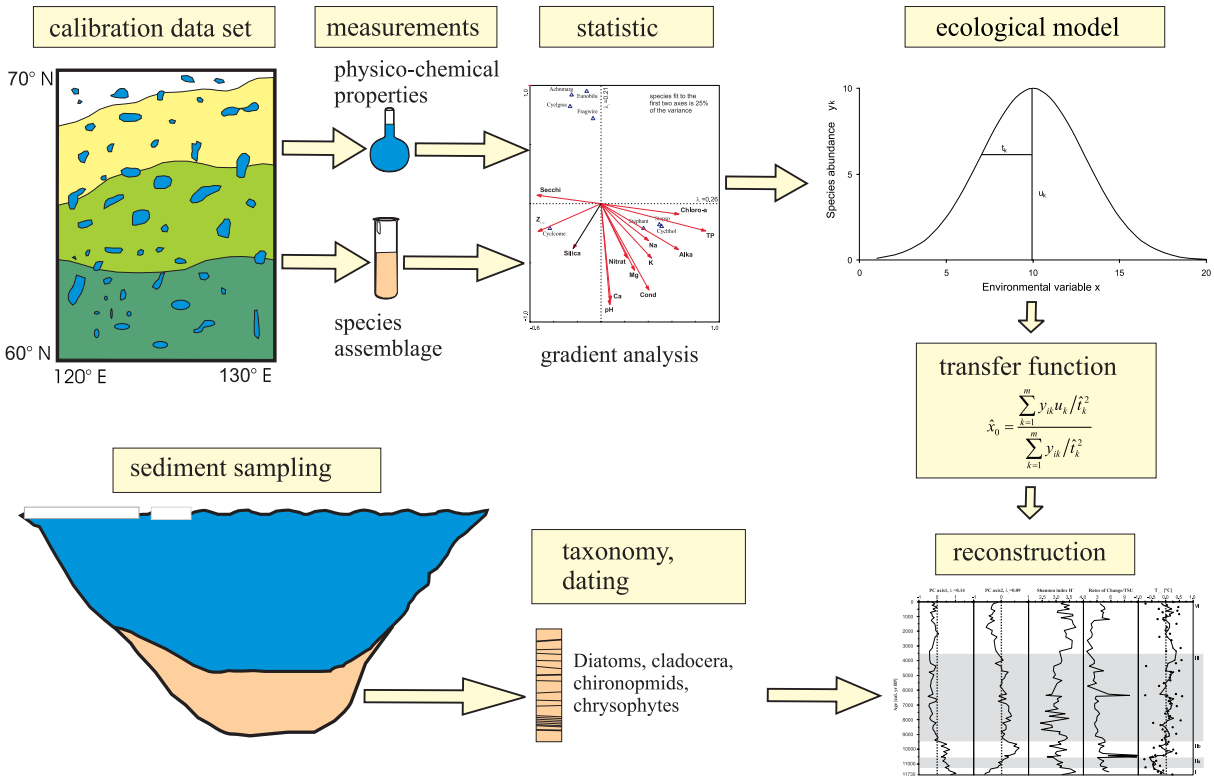


Figure II.1: Schematic overview over the principles of quantitative paleoenvironmental reconstruction of the limnic properties of a water body. From Kumke, unpubl.

- react to only a small set of environmental variables, such as, e.g., temperature and lake-water pH
- react rapidly to environmental change, e.g., have a short generation time and a high dispersal potential
- single species should have specific habitat requirements with narrow tolerances
- they should be ubiquitous and occur in most of the representatives of the ecosystem of interest, e.g., inhabit freshwater lakes and streams etc.
- their remains should be abundant and well-preserved in sediments without a species-specific bias in preservation
- a good taxonomy is needed to ensure the correct relation of species data to environmental data

The biological and ecological properties of the two main bio-indicators used in this study, one of which (chironomids) was used for a quantitative reconstruction, are presented in the following sections.

There are several statistical techniques to reconstruct paleoenvironmental variables quantitatively, some of which assume a linear response of taxa to their environment, others are based upon a unimodal (Gaussian) response model (Birks, 1995). The method applied in this study is **W**eighted **A**veraging **P**artial **L**east **S**quare (WA-PLS), developed by ter Braak and Juggins (1993) and ter Braak et al. (1993). It is a non-linear technique, assuming a unimodal species response to environment, and is one of the most frequently used techniques in quantitative paleoenvironmental reconstructions

(e.g., Walker et al., 1997; Lotter et al., 1997, 1998; Palmer, 1998; Clerk et al., 2000; Brooks and Birks, 2000a; Bigler and Hall, 2002; Larocque and Hall, 2003; Heiri et al., 2003a). WA-PLS has the great advantage that it statistically circumvents the problem of strong secondary gradients (Birks, 1998).

2 Chironomids as paleoenvironmental indicators

Chironomidae (Insecta: Diptera: Nematocera) are often the most abundant insect in aquatic ecosystems (Cranston, 1995). Their aquatic larvae colonise nearly any type of water along a huge gradient of water quality, depth, temperature, elevation, latitude, stream velocity, and other ecological factors. They colonise readily temporary ponds, phytotelmata, and hot springs, some species even thrive in terrestrial, hygropetric and marine environments (Pinder, 1995). The number of species worldwide might be as high as 15,000 (Armitage et al., 1995). Species diversity in any given habitat is often surprisingly high, in large lakes more than 100 chironomid species have been reported (Hofmann, 1988).

There are 10 subfamilies of Chironomidae, five of which occur in Europe's freshwater habitats: The Diamesinae, Prodiamesinae, Orthocladiinae, Chironominae and Tanypodinae. Among the subfamilies, differences in physiology and ecology result in differentiated habitat use. Diamesinae and Prodiamesinae occur almost exclusively in cold, oxygen-rich environments such as rhitral streams, glacier spring brooks and cold oligotrophic lakes. Orthocladiinae show a wider range of distribution, though they are generally related to cool conditions with a high oxygen saturation, and low trophic levels. The Chironominae ('red chironomid larvae') have haemoglobin in their haemolymph fluid that makes them appear blood red. The haemoglobin allows for a more effective oxygen intake of the Chironominae, who consequently dominate habitats with lower oxygen levels, such as potamal streams, the profundal zone of eutrophic lakes and other limnic habitats poor in oxygen supply. The Tanypodinae are the only chironomids that are predominantly predatory. They are most usually found in the littoral of lakes and streams and are like the chironominae usually found under warmer conditions than Orthocladiinae, Diamesinae and Tanytarsini.

Chironomid larvae have four larval stages prior to pupation. The first instar larva ('larvula') is frequently free-living and drifts in the water column. Later instar larvae are free living or dwell in tubes on and in the sediment surface in the littoral or profundal zone of lakes, in plant stems (e.g., *Cricotopus*) or as wood miners (e.g., *Stenochironomus*). Larval development can last for several weeks or up to several years; in temperate regions, chironomids are mostly uni- or bivoltine. The duration of development is a function of food availability and temperature (Tokeshi, 1995). The pupal stage is a comparatively short stage of the chironomid life cycle. The duration may differ from a few hours up to several days. The emerging adult is also short-lived and its behaviour is mainly concerned with reproduction. Emergence of species often occurs more or less synchronised at particular times of the year (Tokeshi, 1995).

Chironomid larvae feed on a variety of food sources. Their different feeding modes comprise gathering, filtering, scraping, shredding and engulfing. Though feeding modes are often assigned to a taxonomical group, e.g., engulfing and piercing is most often described among the Tanypodinae, chironomids as a whole are more appropriately described as opportunistic omnivores. Main food sources

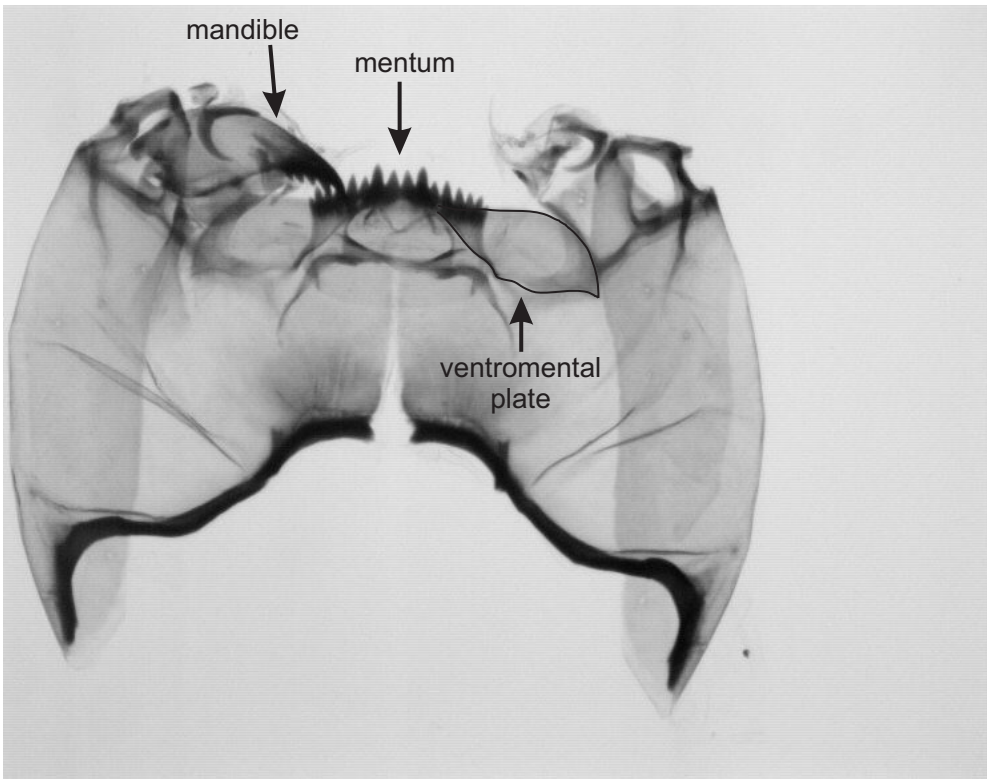


Figure II.2: Ventral view of the larval head capsule of *Sergentia coracina*.

are benthic diatoms, detritus (particulate organic matter), other aquatic insects, zooplankton and oligochaetes, macrophyte material, and sometimes wood debris (Berg, 1995).

The chitinised head capsule of the chironomid larvae is one of the most abundant macrofossils found in lake sediments. Densities of $\geq$ 100 headcapsules cm^{-3} are common (Walker, 1987, 1993). Minimum numbers producing reliable quantitative environmental reconstructions have been set between 50 and 100 head capsules (Quinlan and Smol, 2001; Larocque, 2001; Heiri and Lotter, 2001) per sample. Taxonomy of the subfossil head capsules is based on the morphology of the mentum (a ventral tooth row (Figure II.2) and its accessories), mouth parts, antenna and, especially among the Tanypodinae, head capsule setation. It allows for easy generic identification, and, dependent on the preservation, often species-group and species level.

Chironomid species react to a variety of abiotic factors. Strong determinants are e.g., water temperature, water depth, changes in nutrient load, salinity, and oxygen saturation of the hypolimnion. In several investigations, chironomid assemblages could successfully be linked to water- or air temperature (Walker et al., 1997; Lotter et al., 1997, 1999; Olander et al., 1999; Brooks and Birks, 2000a, 2001; Larocque et al., 2001; Brodersen and Anderson, 2002; Heiri et al., 2003a). Additional studies showed that chironomid assemblages reacted to eutrophication (Brodin, 1982), and changes in oxygen concentration (Clerk et al., 2000; Little et al., 2000), total phosphorus (Brooks et al., 2001) and chlorophyll a concentration (Brodersen and Lindegaard, 1999). Changes in salinity (Walker et al., 1995; Hofmann and

Winn, 2000; Heinrichs et al., 2001) could also be set into relation with midge assemblage changes.

3 Diatoms as paleoenvironmental indicators

Diatoms (Bacillariophyceae) are a group of single-celled aquatic algae that are characterised by a cell wall composed of silica, which is resistant against decomposition after the death of the cell. Diatom taxonomy is based on the frustule (siliceous cell walls) morphology, which are generally well-preserved in sediments and normally allow for identification to the species level. Marine sedimentary records can reach back as far as the Jurassic (Barber and Haworth, 1981), and abundant diatom remains are also found in the sediments of freshwater lakes.

Diatoms are part of the phytoplankton community of lakes, where they occur in pelagic and benthic habitats, growing on stone-, plant-, and sediment surfaces. Strong determinants for diatom community composition northern temperate and subarctic lakes are nutrient concentration, especially total phosphorus concentration (Hall and Smol, 1992, 1999), changes in lake-water pH (Renberg et al., 1993), salinity (Pienitz et al., 1995), and light- and habitat availability (Smol, 1988). Diatoms have been successfully used to reconstruct various chemical and physical variables affecting lake status. Previously, a focus on diatom paleoenvironmental research was put on past acidification trends (Birks et al., 1990; Dixit et al., 1992), and studies like the SWAP programme (**S**urface **W**aters **A**cidification **P**rogramme) could establish significant correlations of diatom deposits from the sediment surface and lake pH of 170 lakes in Great Britain, Norway and Sweden (Battarbee, 1994). The SWAP data forms, together with several other European regional training sets, the European Diatom Database EDDI, a web-based information system to reconstruct surface water acidification and eutrophication (http://craticula.ncl.ac.uk/Eddi/jsp/index.jsp). More recently, studies evaluating the potential of diatom analysis for reconstructing past climate change have emerged (Pienitz et al., 1995; Rosén et al., 2000; Bigler and Hall, 2002, 2003).

Chapter III

Study Area

1 Pre-Quaternary Geology and Topography of Blekinge

Blekinge is a province located in the southeastern part of Sweden. Blekinge makes up the southeasternmost part of the Baltic Shield, also known as Fennoscandia (Figure III.1). The predominant pre-Quaternary stratigraphical units of Blekinge consist of granitoids and gneisses of mainly Middle Precambrian age (Wiklander, 1974). Within the region of the study sites, four geological units can be distinguished: 1. The Blekinge coastal gneisses, 2. Gneissic granite, also called Tving granite (Wiklander, 1974), 3. the Spinkamåla granite and 4. the Karlshamn granite (Pousette et al., 1983). Wiklander (1974) suggests an age of 1280 m.y. for the coastal granite. The Stora Kroksjön and Lilla Torkelsjön study sites lie within the Tving granite outcrop area (Fig. III.2).

Blekinge is divided into four step-like topographical sections: 1. the northern Blekinge plain with elevations above 100 m above sea level (a.s.l.), 2. river valley landscape aligned NNW-SSE, where the elevation rises steeply from about 30 m to 100 m a.s.l., 3. coastal plain with archipelago and 4. the East Blekinge plain (Björck, 1979) (Figure III.1 A-D). The typical, uneven topography was created by glacial and fluvial erosion following fractures preformed by deformation (Larsson, 1954).

2 Quaternary Geology and shoreline displacement

2.1 Quaternary deposits

The Quaternary deposits in the coastal area of Blekinge consist of a relatively thin till layer with abundant bedrock exposures, and below the highest shore line (see below), the till is covered with varved clay and silt in the basins and valleys. Above the highest shore line, the till is generally thicker, and areas of hummocky moraines and transverse moraine ridges are characteristic (Björck and Möller, 1987). Glaciofluvial deposits are mainly found in the valleys and show a gradient from fine silt and sand below ca. 55 m a.s.l. to coarser fractions at higher levels (Ising, 1998; Lagerlund and Björck, 1979).

2.2 Shoreline processes

During the Pleistocene and Holocene, Blekinge's shoreline fluctuated considerably. This has been documented by numerous investigations (e.g., Berglund, 1966a; Björck, 1979; Liljegren, 1982; Svensson, 1991; Björck and Digerfeldt, 1991) for over a century (Ising, 2001). The shoreline displacement stemmed from two geological processes; when the Scandinavian iceshield melted in the late Pleistocene, the lowered pressure on the Scandinavian shield resulted in an isostatic land uplift. Concurrently, world-

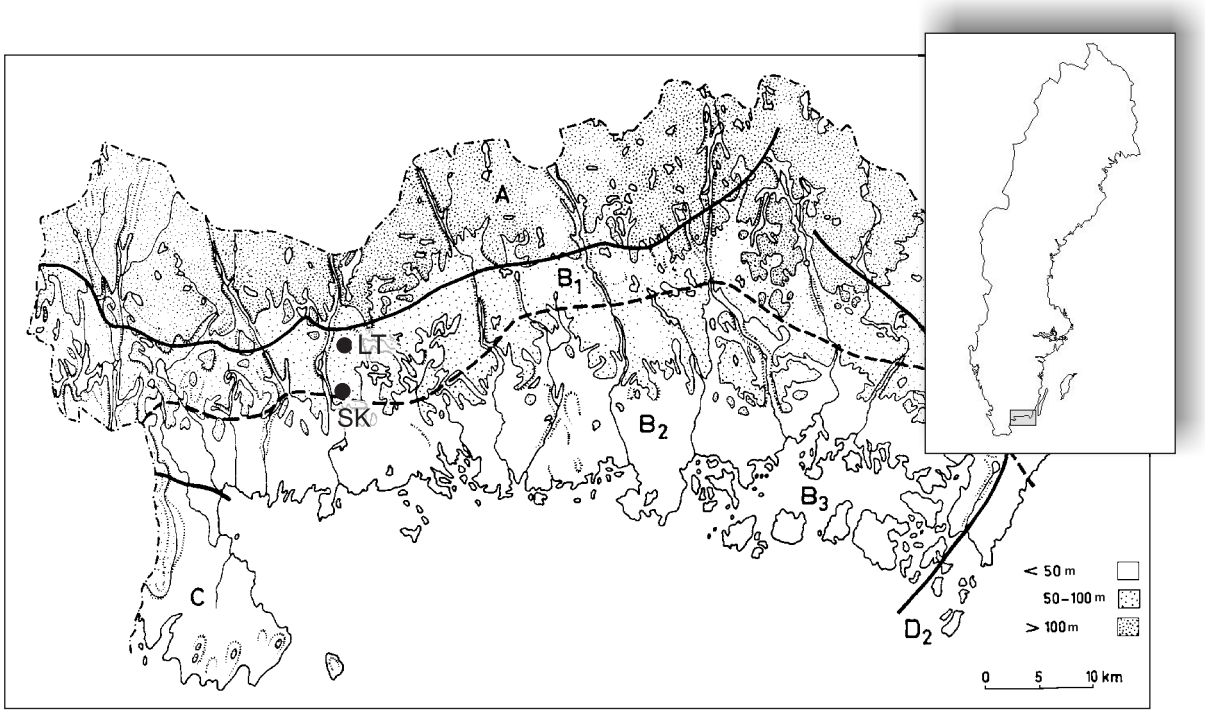


Figure III.1: The location of the two investigated lakes (LT, Lilla Torkelsjön and SK, Stora Kroksjön) in the Province of Blekinge. Topographic regions of Blekinge: A. the northern plain, B1. the valley landscape, B2. the coastal plain, B3. the archipelago, C. the Listerlandet peninsula, D. the East Blekinge plain. White and sparsely and densely dotted areas denote increasing elevation. Redrawn from Berglund (1966a)

wide eustatic sea level fluctuations occurred. These two processes resulted in a temporal and spatial heterogeneous pattern of transgressional and regressional phases along the coast of the Baltic Sea. The highest former shore line of the Baltic Sea in Blekinge is placed at about 65 m a.s.l. (Ringberg, 1971, 1991; Björck, 1979, 1995; Berglund et al., 1996). One of the investigated lakes, Stora Kroksjön, lies at 51 m a.s.l. and was a part of the Baltic Ice Lake before isolation occurred around 14,000 cal. yrs BP.

2.3 History of the Baltic Sea

The development of the Baltic Sea and its hydrological predecessors is characterised by the interaction of the aforementioned geological processes, meltwater discharge into the basin and drainage. Though some stages of the Baltic Ice Lake are still not entirely understood, Björck (1995) gives a thorough overview of the processes after ca. 14,000 cal. yrs BP, summarised below.

Ice retreat and the Baltic Ice Lake stage

Late-Pleistocene ice-retreat is considered to have been rapid (Björck and Möller, 1987). The Blekinge coast was deglaciated around 14,800 cal. yrs BP, and Blekinge and adjacent regions, such as southern Småland, became deglaciated during the Bølling chronozone, between 14,800 and ca. 14,500 cal. yrs BP (Lundqvist and Wohlfarth, 2001).

After ice recession, the southern part of the Baltic basin was filled with meltwater from

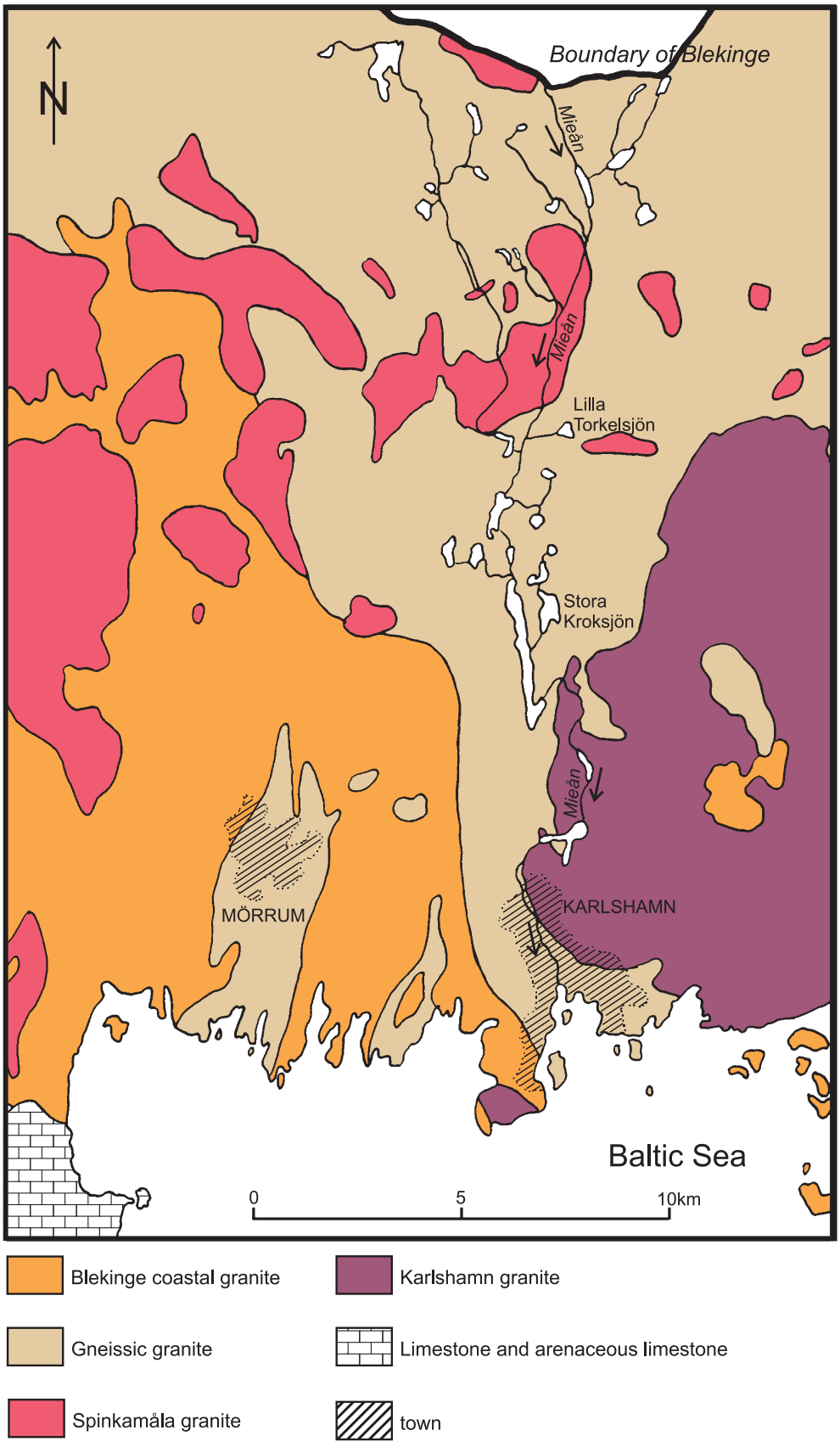


Figure III.2: Pre-Quaternary geology of the study site region. Arrows mark the direction of water flow. Redrawn from Pousette et al. (1983).

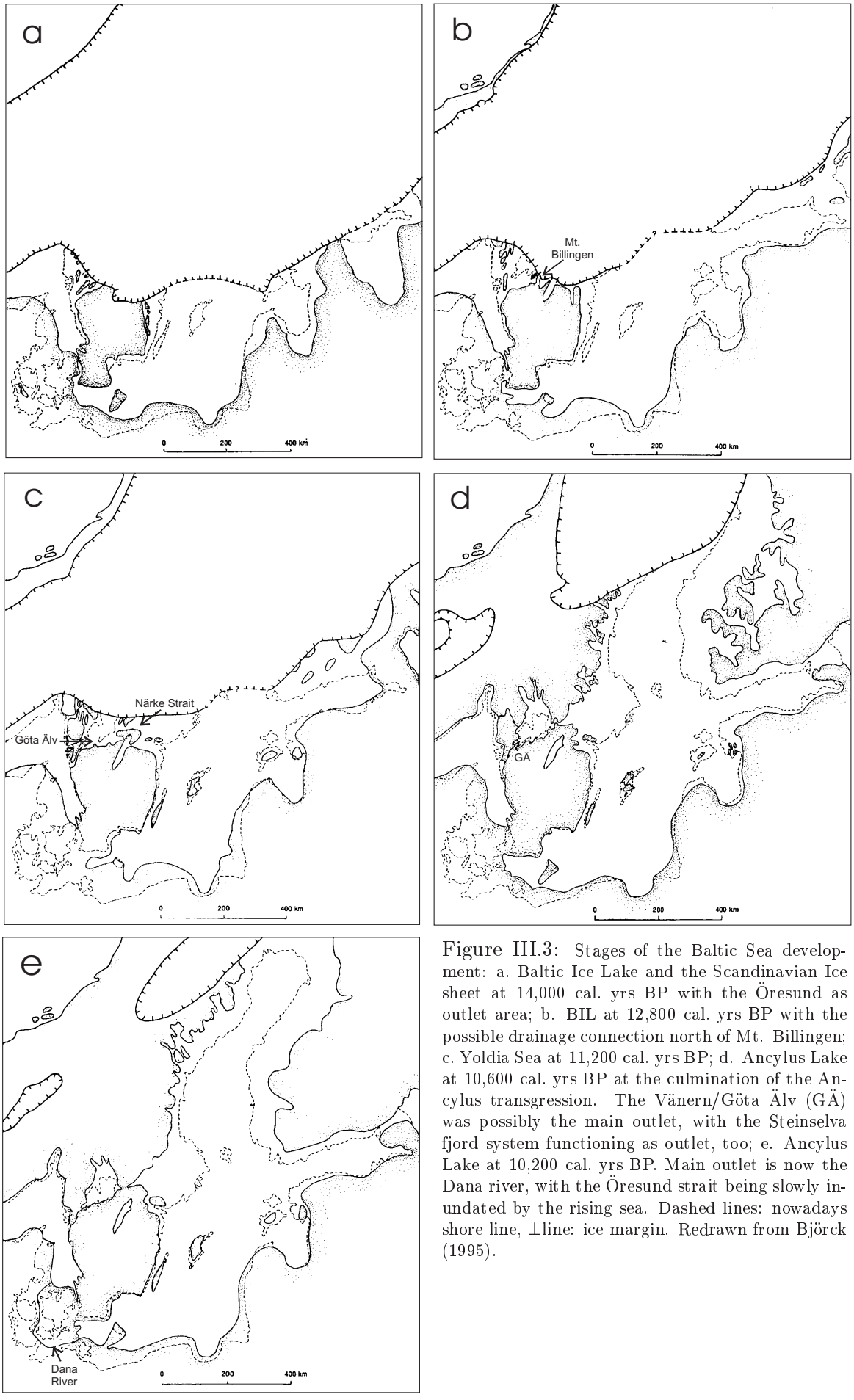


Figure III.3: Stages of the Baltic Sea development: a. Baltic Ice Lake and the Scandinavian Ice sheet at 14,000 cal. yrs BP with the Öresund as outlet area; b. BIL at 12,800 cal. yrs BP with the possible drainage connection north of Mt. Billingen; c. Yoldia Sea at 11,200 cal. yrs BP; d. Ancylus Lake at 10,600 cal. yrs BP at the culmination of the Ancylus transgression. The Vänern/Göta Älv (GÄ) was possibly the main outlet, with the Steinselva fjord system functioning as outlet, too; e. Ancylus Lake at 10,200 cal. yrs BP. Main outlet is now the Dana river, with the Öresund strait being slowly inundated by the rising sea. Dashed lines: nowadays shore line, ⊥line: ice margin. Redrawn from Björck (1995).

the receding Weichselian ice sheet. This water body - the Baltic Ice Lake 'BIL'- (Björk, 1995; Jensen et al. 1997) existed until 11,560 cal. yrs BP (Wohlfarth et al., 1993) and was subject to significant water level fluctuations. Because of uneven isostatic uplift, the highest shoreline forms a highly heterogeneous pattern throughout southern Scandinavia. In Western Blekinge, it is commonly found between 55 and 65 m a.s.l. (Berglund, 1966a; Björck, 1979; Ringberg, 1979). The highstand directly after deglaciation was followed by an initial gradual lowering of water level by about 10 m. A more drastic event, called the first drainage, occurred around 12,800 cal. yrs BP, and led to a lowering of the water level by another ca. 25 m. The drainage probably occurred through the Öresund Strait (Figure III.3a, Björck, 1979; 1995) and left the lake level at values of between 30 and 20 m above current sea level.

Around 13,000 cal. yrs BP, the main drainage channel changed and was now through the so-called Närkestrait, directly south of the margin of the retreating ice shield (Figure III.3b). As no saltwater ingression had taken place, it is possible that this drainage was mainly subglacial. Several transgressions and regressions followed, caused by dammed and newly eroded outlets e.g., in the Öresund region and oscillating ice margins during the Younger Dryas. Around 11,560 cal. yrs BP, the final drainage of the BIL happened in a dramatic lowering of another 25 m. This marked the end of the BIL stage, when the ice margin damming the BIL north of Mt. Billingen gave way to the water masses.

Yoldia Sea stage

The final drainage of the Baltic Ice Lake marks the onset of the so-called Yoldia Sea stage (ca. 11,560–10,700 cal. yrs BP) and is more or less synchronous with the end of the Younger Dryas stadial and the beginning of Holocene warming (e.g., Björck, 1981; Björck and Digerfeldt, 1995). The lowered water level opened a landbridge connecting Germany, Denmark and Sweden, with very low shore levels of ca. -30 m a.s.l., but the ongoing subsidence of the southern Baltic basin lead again to marine transgression. North of a narrow eustatic region, continuing land uplift resulted in regression along the Scandinavian coast. Thus, a further shoreline lowering along the Swedish coast can be observed. Despite the ongoing land uplift, a salt water intrusion through the Närke Strait-region occurred between 11,300 and 11,100 cal. yrs BP (Figure III.3c), probably as a result of rapid sea-level rise in response to high global meltwater discharge (Bard et al., 1996). The short brackish phase in the Yoldia Sea can be identified by fossil diatoms and molluscs, such as *Portlandia (Yoldia) arctica* (e.g., Fredén, 1988; Björck and Digerfeldt, 1986). The brackish phase ended when for reasons not entirely clear, the Närke Strait became too narrow for salt water intrusion. Lake Vänern remained connected with the Baltic basin, draining through the large River Göta Älv. This was the case around 10,700 cal. yrs BP.

Ancylus Lake stage

The Ancylus Lake stage (ca. 10,700–9800 cal. yrs BP), named after the index fossil *Ancylus fluviatilis*, a freshwater mollusc, is regarded to be the most complicated stage of the Baltic Sea development in terms of outlet areas and water levels. Björck (1995) distinguishes three stages: The Ancylus transgression phase, which culminated around 10,600 cal. yrs BP, the Ancylus regression until ca. 10,200 cal. yrs BP and the non-dammed Ancylus stage from 10,200 until ca. 9800 cal. yrs BP.

For the period from 10,700–10,200 cal. yrs BP, the Ancylus Lake drained still through the Närke Strait - Lake Vänern region. The two main outlets were the Steinselva River and the Göta Älv (Figure III.3d), with the latter being the most important. As this area was still under ongoing uplift, the Ancylus Lake rose in pace with the lifting threshold, causing a significant transgression in the southern part of the Baltic basin, where uplift had either almost ceased or even turned into subsidence. All along the German and Polish coast, land that just recently had emerged from the Yoldia Sea was flooded again. From around 10,600 cal. yrs BP, erosion through the Darss Sill area, southwest of the Öresund region (Figure III.3d) between Fehmarn and Lolland, allowed water to flow north along the eastern side of Langeland and through the Store Belt, reaching the sea in the southernmost Kattegatt. Through this channel (the Dana River), which still exists as a sub-marine canyon system, more and more water drained, eroding it ever deeper, whereas the two northern outlets gradually ceased to function with the falling water levels. From ca. 10,000 cal. yrs BP on, the Ancylus Lake level had lowered so much that it was level with the sea and the Närke-Segefors threshold area had emerged, forming a new landbridge to southern and northern Fennoscandia. This isolated Lake Vänern from the Baltic basin and made it the largest inland lake of Sweden. The importance of the two northern outlets, the Göta Älv and Steinselva, diminished gradually as the Dana River started to function as an outlet (Figure III.3e), though the Göta Älv remained the outlet of Lake Vänern.

The transition from the Ancylus Lake to the Littorina Sea *sensu lato* is marked by evidence of a weak brackish phase, such as marine and brackish-water diatoms, between 9800 and 8500 cal. yrs BP. Isostatic movements are continuing to this very day, ever changing the shore line of the Baltic Sea. However, these shore line displacements are not as significant as earlier. Stages distinguished from 9800 cal. yrs BP until present are mainly characterised by changes in the salinity of the Baltic Sea, for example the Mastogloia-, Littorina- and Limnea stages.

3 Recent Climate

Blekinge has a temperate oceanic climate, established by the warm waters of the Gulf stream. Weather usually is governed by a low pressure over the Atlantic Ocean and a high pressure over the Baltic Sea. The study site region received an annual precipitation of between 650 and 700 ml between 1931-1960 (Pousette et al., 1983). The closest weather station (Grimsmåla, Swedish Meteorological and Hydrological Insititute (SMHI) station nr. 6420) registered a mean July air temperature of 16.3 °C between 1961 and 1990 (Swedish Meteorological and Hydrological Institute, pers. comm.). Mean annual temperatures lie around 7 °C. The duration of the annual vegetation period is about 240 days.

4 Study Lakes

The two study lakes, Stora Kroksjön and Lilla Torkelsjön, are located within 5 kilometers of each other on the valley landscape (see Chapter III.1) topographical section of Blekinge, about 8 kilometers north of the seaside town of Karlshamn. They both belong to the Mieån River drainage system that drains the meteorite crater lake Mien about 20 km north of the study site. Both catchments are thought to have never been subject to extensive clearing, though marked changes in the tree composition took place in the beginning of the 19th century (Björk

Table III.1: Morphometric and physico-chemical characteristics of Lakes Stora Kroksjön and Lilla Torkelsjön. Physicochemical data were measured in May 1998. * DOC was measured by the Blekinge Länstyrelsen

	area [ha]	catchment size [ha]	maximum depth [m]	altitude [m a.s.l.]	pH	conductivity [μS cm^{-1}]	chlorophyll a [mg m^{-3}]	DOC* [mg L^{-1}]
Stora Kroksjön	26	340	23	51	7.4	108	4.2	15
Lilla Torkelsjön	8	40	11	73	6.8	73	4.7	n/a

et al., 1998). The southward spreading of pine (*Pinus*) and spruce (*Picea*) forest into Blekinge occurred after the end of the 17$^{\text{th}}$ century, when a map records beech (*Fagus*) forest as the main forest vegetation.

Both lakes have in recent years (1986 and 1990) been subject to liming in order to counteract acidification caused by atmospherical pollution (Miljövårdsverket, pers. comm., Björk 1996). Today, both lakes are circumneutral in pH. Morphometric and physico-chemical characteristics of both lakes are given in Table III.1.

4.1 Lake Stora Kroksjön

Stora Kroksjön (56°14'82"N, 14°51'59"E) (Figure III.4), a deep mesotrophic lake, is located in the Långasjönäs nature reserve recreation area five kilometers north of Karlshamn. Its maximum depth is ca. 23 m and its surface area is 26 ha. The catchment has a size of about 340 ha and is covered with a mixed beech and spruce forest, as it lies on the edge of the southward spreading spruce forest region (Lindquist, 1959). Lake Stora Kroksjön has two above-ground inflowing streams, one located in the northern edge from Lake Lilla Kroksjön, and a small inflow on the eastern side. An outflow is located at the southwestern edge of the lake and drains into Lake Långasjön.

Lake Stora Kroksjön becomes thermally stratified during the summer and exhibits moderate oxygen depletion in the hypolimnion (Figure III.5). The clinograde vertical profile of oxygen concentration and temperature points towards meso- to eutrophic conditions (Åberg and Rohde, 1942). Total phosphorus concentrations have risen from < 10 mg m^{-3} in the 1960's and 1970's to 83 mg m^{-3} in 1981.

Lake Stora Kroksjön hosts the crustaceans *Mysis relicta*, *Monoporeia affinis* and *Pallasea quadrispinosa* which are relicts of the Baltic Ice Lake (BIL) and, in Sweden, are typically found in lakes below the former highest coast line (Thienemann, 1950). Lake Stora Kroksjön lies 51 m a.s.l. below the former highest shore line of the BIL and was disconnected from it in the Bölling chronozone, during an initial slow lowering prior to the first rapid drainage (see Chapter III.2.3), when the BIL level dropped to levels of 45 m a.s.l. (Berglund, 1966a).

Lake Stora Kroksjön has been treated with Rotenon in the early 1960's in order to eliminate the existing fish community and to replace it with an artificial one (Björk et al., 1964).

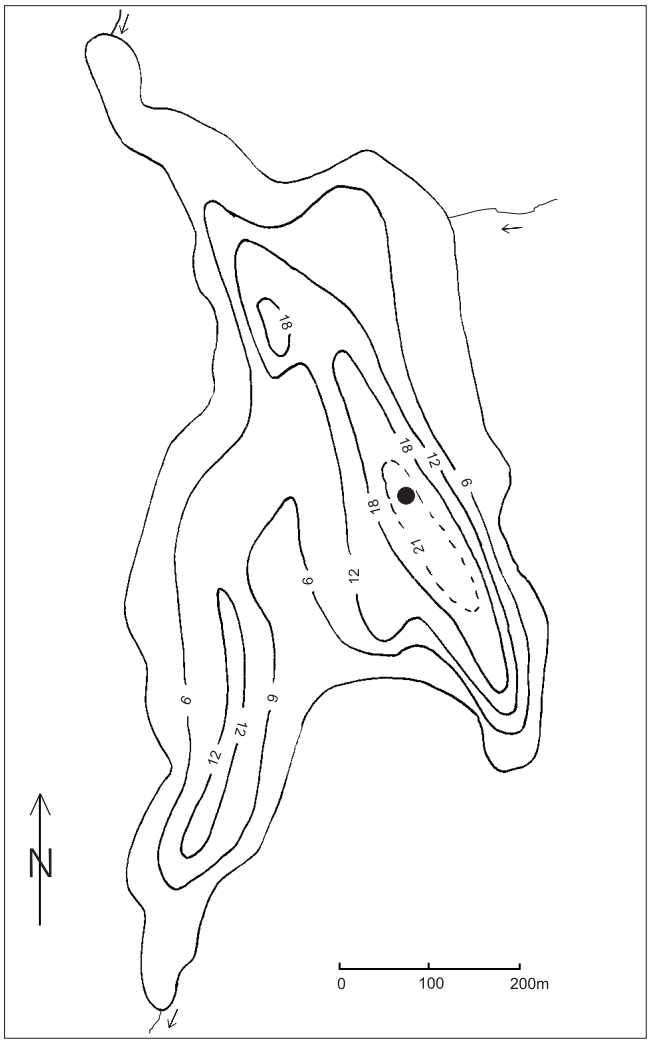


Figure III.4: Bathymetric map of Stora Kroksjön; the dot indicates the coring site.

4.2 Lake Lilla Torkelsjön

Lake Lilla Torkelsjön (56°17'10"N, 14°51'89"E) is a small, shallow lake (Björk, 1996) with a maximum depth of ca. 11 m and a surface area of about 8 ha (Figure III.6). It has a catchment of about 40 ha and lies at an elevation of 73 m a.s.l.. Lilla Torkelsjön is groundwater-fed and has no above-ground inflow. The small outflow is at the southwest edge of the lake and drains into the Mieån River. No detailed measurements of oxygen concentration, temperature gradients, dissolved organic carbon (DOC) or total phosphorus concentration (TP) were available. Lilla Torkelsjön is surrounded by spruce forest.

The liming of Lilla Torkelsjön has resulted in a change of macrophyte community structure (Björk et al., 1998). The lake was earlier dominated by *Littorella uniflora*, *Isoëtes lacustris* and *Lobelia dortmanna*, whereas today *Chara delicatula* can be observed.

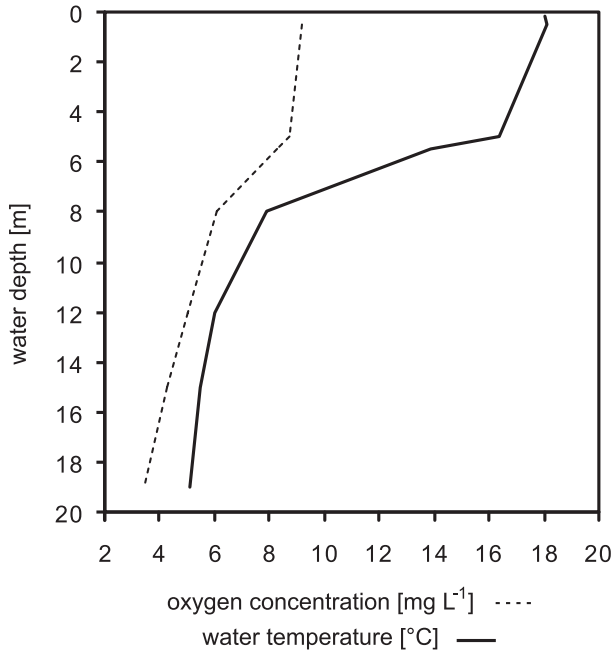


Figure III.5: Vertical distribution of oxygen concentrations and temperatures in Lake Stora Kroksjön, July 1970.

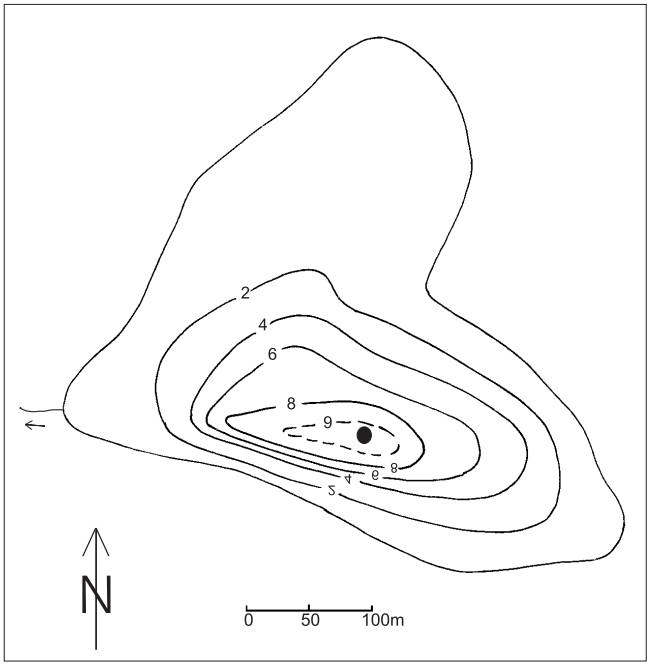


Figure III.6: Bathymetric map of Lilla Torkelsjön; the dot indicates the coring site.

Chapter IV

Methods

1 Coring

The sediment cores were taken from Lakes Stora Kroksjön and Lilla Torkelsjön between November 22th and 26th, 1998, using a piston corer (company Niederreiter, Austria). Cores were removed from the deepest part of the lake, which had been located using echo sound. The plexiglass core tubes had a length of 2 m and an inner diameter of 8.6 cm. At Lake Stora Kroksjön, four cores with an overlap of 50 cm to 1 m were taken. At Lilla Torkelsjön, three cores with an overlap of 1 m were taken. The cores were stored at a temperature of 4 °C prior to subsequent analysis.

The cores were pressed out of the tubes into a fitting half pipe, cleaned on both sides and described. Sediment symbols in diagrams follow the modified Troels-Smith system (Troels-Smith, 1955; Aaby and Berglund, 1986). The cores were sub-sectioned into 2.5 cm intervals. The samples were stored in small, air-tight plastic containers at 4 °C until further processing. Sediment needed for subsequent analysis was removed from the containers directly prior to processing.

2 Loss on ignition

From each sample, sediment was used for measuring loss on ignition (LOI) in order to determine stratigraphic correlation. LOI is a standard technique for measuring the content of organic carbon in sediments as the weight loss after combustion at 550 °C (Dean, 1974; Bengtson and Enell, 1986). A volume of 5 ml wet sediment was dried for 24 h at 120 °C, weighed, then combusted at 550 °C for 3 h and re-weighed. Carbonate content of the sediment was expected to be negligible because of the presence of granitoid/gneiss bedrock within the whole catchment and low lake water pH. Therefore, a measure of LOI at 950 °C was not performed. A continuous LOI curve of the cores of each lake was generated by averaging the values of the overlapping parts of the sequences.

3 Dating

From each lake, six samples were dated by the Radiocarbon Dating Laboratory of Lund University. In all cases, terrestrial material (leaves and bark) was dated for conventional radiocarbon dates. The results are given in calibrated years before present (henceforth abbreviated as 'cal. yrs BP'), calculated with a half-life of 5568 years. Reference date for 'present' is the year 1950 A.D.. The calibration was done by using the software BCal, an on-line bayesian calibration tool of the University of Sheffield (URL: http://bcal.shef.ac.uk). The calibration tool uses the IntCal98 calibration curve (Stuiver et al., 1998). The age-depth-model was calculated using linear interpolation of the calibrated ages between dated samples.

The chronozone boundaries applied in this study are those of the latest revision of

the pollen stratigraphy chronology in southern Sweden (Gaillard et al., 1996). For ages prior to the Younger Dryas/Preboreal transition, the **G**reenland **I**ce-**C**ore **P**roject 'GRIP' oxygen isotope record event stratigraphy is used (Björck et al., 1998; Walker et al., 1999). The chronozones used are: OD (Older Dryas syn. GI-1d GRIP event, 14,050-13,900 cal. yrs BP), AL (Allerød syn. GI-1c - GI-1a GRIP event, 13,900-12,650 cal. yrs BP), YD (Younger Dryas syn. GS-1 GRIP event, 12,650-11,500 cal. yrs BP), PB (Preboreal, 11,500-9900 cal. yrs BP), BO1 (Early Boreal, 9900-8800 cal. yrs BP), BO2 (Late Boreal, 8800-7800 cal. yrs BP), AT (Atlanticum, 7800-5700 cal. yrs BP), SB (Subboreal 5700-ca. 2600 cal. yrs BP), and SA (Subatlanticum ca. 2600 cal. yrs BP until present day) (Mangerud et al., 1974; Skog and Regnéll, 1995; Gaillard et al., 1996; Björck et al., 1998). The Atlanticum/Subboreal border corresponds to the Mesolithic/Neolithic border, the Early/Late Subboreal border corresponds to the Neolithic/Bronze Age border and the Subboreal/Subatlanticum border corresponds to the Bronze Age/Iron Age border (Berglund et al., 1991).

4 Chironomid analysis

Sediment samples were deflocculated in 10% KOH for 30 minutes at 80 °C, then washed through sieves of 200 μm and 100 μm with distilled water. The residue was poured onto a petri dish with an underlying grid of 5x5 mm and sorted under a stereo microscope with 20x magnification. Head capsules were picked using Pasteur pipettes treated with Silicone oil type 3, preventing the capsules from getting stuck to the glass within the pipette.

Sediment sample size ranged between 3 and 50 ml of wet sediment in order to generate at least 100 head capsules. Samples which contained less than 50 head capsules were excluded from the analysis (Hofmann, 1986; Larocque, 2001; Heiri and Lotter, 2001). If a sample had an unexpectedly high head capsule density, the first ca. 50 head capsules of each fraction were picked and mounted in order to obtain an unbiased species composition while the remaining head capsules were only counted. Half a mentum was counted as 0.5 specimen, more than half a mentum was counted as one specimen, less than half a mentum was ignored. Head capsules were mounted on a permanent slide ventral side up in Hydro Matrix ®.

The head capsules were identified with reference to Hofmann (1971b), Sæther (1975), Wiederholm (1983), Pillot and Buskens (1984), Kowalyk (1985), and Rieradevall and Brooks (2001). Identifications were verified by cross-checking with the Norwegian calibration set (Brooks and Birks, 2000a).

The results of the chironomid analysis are presented as percent abundance diagrams using the computer program psimpoll Version 4.01, written by Keith D. Bennett.

5 Diatom analysis

Diatom preparation and identification was carried out by Prof. Dr. Andrzej Witkowski at the Department of Marine Science at Szczecin University, Poland, following standard procedures (Berglund and Ralska-Jasiewiczowa, 1986). The data presentation and analysis was performed by the author of this study. The results are presented as percent abundance diagrams using the computer program psimpoll Version 4.01, written by Keith D. Bennett.

6 Pollen analysis

Pollen samples were prepared by Anna Lindahl at the Quaternary Geology Department, Lund University, using 1 cm^3 according to standard methods (Berglund and Ralska-Jasiewiczowa, 1986; Faegri et al., 1989). The results were zoned by the analyst and Prof. em. Gunnar Digerfeldt (Quaternary Geology Department, Lund University, Sweden). The data was processed with the software Tilia and presented with the software Tilia.Graph Version 2.0.1, written by E. Grimm. The graphs were drawn by the analyst.

7 Statistical analysis

Statistical analyses were subsequently performed on square-root transformed data (except for diversity indices and rarefaction analysis) to objectively determine where patterns of change exist within the data set. Chironomid and diatom taxa not reaching a proportion of 0.5 % in at least one sample were excluded from the analyses. This never occurred within the chironomid samples. Among the diatoms, 141 taxa were excluded from Lake Stora Kroksjön (with 204 taxa remaining) and 91 taxa from Lake Lilla Torkelsjön (195 remained).

7.1 Zonation

Major changes in the fossil chironomid and diatom assemblages were confirmed using constrained cluster analysis by sum of squares (CONISS). CONISS is a agglomerative cluster analysis method that is constrained to use stratigraphically adjacent samples (Grimm, 1987). The minimum number of significant zones in the stratigraphy was tested using a broken-stick model (Bennett, 1996). The test involves comparing the variances of each zone against the expected variance from a broken stick model (i.e., the variance of a stick segment derived at random). As dissimilarity index, chord distance was used. Zonation was carried out using the zone option of the computer program psimpoll Version 4.10 from Keith D. Bennett and tested with the computer program bstick Version 1.0 written by H.J.B. Birks. Deviating from this procedure, for the pollen data, the zonation provided by the analyst was adopted.

7.2 Diversity indices and rarefaction

Diversity indices were used to describe species richness, diversity and evenness in the chironomid samples. Half head capsules were counted as one specimen.

Species diversity was calculated using the Shannon-Weaver index (*H'*):

$$H' = -\sum_{i=1} (p_i \cdot \ln p_i)$$

where p = the proportion of the i^{th} species of the total count (Shannon and Weaver, 1949). Evenness is a measure of how similar the abundances of different species are. When there are similar proportions of all species, evenness is one. When the abundances are very dissimilar, the value increases. Species evenness was calculated using Pielou's index (*J'*):

$$J' = H'/H_{max}$$

where H_{max} is the maximum diversity if all species were evenly distributed (Pielou, 1975).

Species richness depends in part on the number of individuals counted in a sample. Rarefaction analysis makes species richness comparable even with different count sizes in each sample (Birks and Line, 1992). The process gives an estimate of how many species would have been found, if count sizes had been equal in all samples, based on the lowest count size of all compared samples. A statistical assumption made when using rarefaction is that the proportion of counted individuals of a given sample is representative for the assemblage in that sediment sample (Birks and Line, 1992). As the number of head capsules found, counted, and determined differed between samples (from a minimum of 53 to 201.5 maximum determined), rarefaction was carried out. The calculation was performed using the software EcoSim Version 7.30 by Gotelli and Entsminger (2003). The software was run with 5000 Monte Carlo iterations. The lowest count sum in Stora Kroksjön was 53 head capsules, in Lilla Torkelsjön, 74 head capsules was the lowest count.

7.3 Rates of change

Rates of community compositional change between samples were quantified using chord distance per 100 years time standardisation unit (TSU), using age-weighted average as smoothing parameter. Prior to calculating rates of change, species data were interpolated at linear 100 year intervals. 95 % confidence limits were estimated from the fossil data using randomisation with 5000 Monte Carlo permutations. Rates of change within the chironomid stratigraphy were determined using the software ratepol Version 0.8 (Jacobson and Grimm, 1986). The diatom assemblages were reduced to the 100 most abundant species, as ratepol processes a maximum number of 100 species.

7.4 Principal Components Analysis

A principal component analysis (PCA) was used detect major trends and gradients in the species data sets (chironomids, diatoms and pollen). PCA is an indirect eigenanalysis technique to reduce the dimensionality of a data set. It constructs the theoretical variable that minimises the total residual sum of squares after fitting straight lines to the species data. PCA does so by choosing the best value for the samples, the sample scores. In the bi-plot, it recalculates the position of the data points and rotates them such that the maximum variability is visible. Doing so, a theoretical explanatory variable is estimated from the species data alone. More variables (=PCA axes) can be constructed under the constraint that they are uncorrelated to previous PCA axes.

Data was analysed focusing on inter-sample distance without post-transformation (scaling -1). The data were square root transformed prior to analysis. PCA was calculated using the software CANOCO Version 4.02 by C. ter Braak and P. Ŝmilauer.

7.5 Temperature reconstruction

For reconstructing past climate development, a chironomid-based mean July air temperature transfer function developed by Brooks and Birks (2000a; 2001) was applied to the midge record of both study lakes. The calibration data set in the state used in this study comprises the modern taxon and environmental data of a set of 153 lakes from southern Norway (58 °N) up to Svalbard (Spitzbergen, 80 °N). The temperature gradient spanned from 3.5–16.0 °C in an altitudinal range from 0–1600 m. Temperature data were derived from between 10 and

Table IV.1: Performance statistics of the mean July air temperature inference model showing different WA-PLS components. RMSEP: Root mean square error of prediction. The model that has the lowest RMSEP combined with a low maximum bias and a high R^2 was chosen.

Components	RMSEP	R^2	Maximum Bias
1	1.4955	0.8216	1.9040
2	1.0765	0.9016	1.0835
3	1.0119	0.9129	1.1664
4	1.0396	0.9088	0.9710
5	1.0687	0.9035	0.9685
6	1.1406	0.8927	1.0044

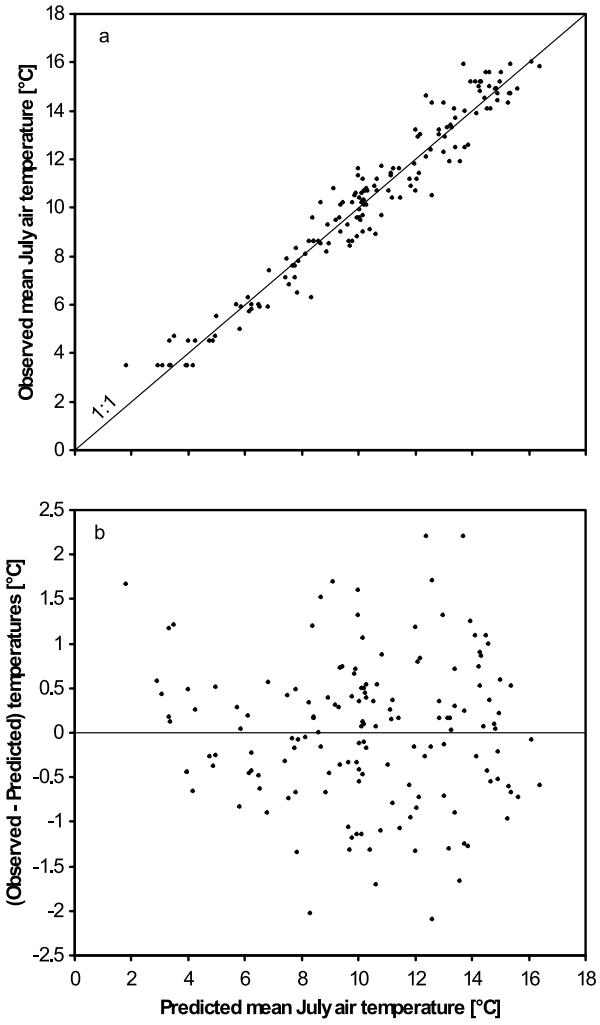


Figure IV.1: (a) Observed mean July air temperature in 153 Norwegian lakes plotted against predicted chironomid-inferred mean July air temperatures using a 3-component WA-PLS model based on leave-one-out cross-validation. (b) Residual temperatures plotted against predicted mean July air temperature. Data from Brooks and Birks, unpublished. Data presented according to Racca and Prairie (2004).

20 meteorological stations situated close to the lakes, averaged over 30 years and corrected for distance from coast and altitude (Brooks and Birks, 2000a, 2001). At all sites, 14 environmental variables were measured next to the species composition of the modern chironomid assemblage including: mean July air temperature (MJAT), water temperature, water depth, pH, alkalinity, K^+, Ca^{2+}, Mg^{2+}, Na^+, Cl^-, SO_4^{2-}, NO_3^-, total organic carbon (TOC), and conductivity (Brooks and Birks, 2000a, 2001). The data set incorporates 140 chironomid taxa. In this model, MJAT explained the highest amount of variation within the chironomid species assemblages in a Canonical Correspondence Analysis (CCA).

The model produces the lowest root mean square error of prediction (RMSEP) in combination with a low maximum bias as a 3-component WA-PLS (**W**eighted **A**verage–**P**artial **L**east **S**quare) regression model (ter Braak and Juggins, 1993; Birks, 1995), calculated with the software WAPLS Version 1.5 written by Steve Juggins and Cajo ter Braak. Table IV.1 summarises the performance statistics of the various transfer functions. Figure IV.2 presents all taxa present in the Norwegian calibration set that were found in the sediments of Lakes Stora Kroksjön and Lilla Torkelsjön, arranged according to increasing modelled temperature optima.

The root mean square error of prediction (RMSEP) was determined by the leave-one-out cross-validation method ('jackknifing') (ter Braak and Juggins, 1993). In this procedure, one object i is removed from the data set. The regression is then re-calculated with $n-i$ objects and the fitted model used to predict i. The difference between the full and the $n-i$-model is calculated and the whole process repeated for all n objects of the data set. From the error estimates, the RMSEP is calculated (Birks, 1995).

The temperature reconstruction scatter plots resulting from the Norwegian calibration set applied to the Blekinge fossil chironomid data were smoothed with a LOWESS ('locally weighted regression') smoother, which performs a series of regressions over small areas of the plot. The span parameter was set at 0.25. The LOWESS was calculated using the software STATVIEW Version 5.0.

7.6 Sample-specific error

The sample-specific error is generated additionally to the RMSEP. It is based on the results of the cross-validations of the transfer function, using the so-called bootstrapping-technique. In bootstrapping, n samples are randomly chosen, based on the distribution of the calibration data set. Some samples may be chosen repeatedly, while others may be excluded. With this synthetically generated data set, weighted averaging regression and calibration is performed. An estimated value for the variable to reconstruct x_0 is generated. Samples not included form a test data set and for these samples, another estimate value (x_i) is computed. The bootstrap procedure is repeated several thousand times. Thus, the standard deviation of the estimate for x_0 is calculated, and equals the error generated by incorrect estimate of optimas and tolerances during the regression (s_{i1}). This error varies between samples. Furthermore, the mean of the estimated x_i from the bootstrap cycles is calculated and compared with the measured x_i of the respective samples of the test set. The square root of the mean squared differences between $x_{i\ measured}$ and $x_{i\ estimated}$ results in the error component s_{i2}. This component is constant over all samples, as it is derived only from the calibration data set. The sample-specific error is calculated from both components:

Figure IV.2: Modelled species temperature optima (°C) of all taxa present in the sediment cores of Lakes Stora Kroksjön and Lilla Torkelsjön.

$$e_{sam} = \sqrt{(s_{i1}^2 + s_{si2}^2)}$$

It integrates the prediction error as well as the calibration error. Sample-specific errors are shown for the midge-inferred temperature estimates (Figures V.13 and V.15).

7.7 Modern analogues

Similarity between modern samples from the Norwegian calibration set (see Chapter IV.7.5) and fossil data was calculated using the dissimilarity between the fossil taxa and the taxa of the calibration data set:

$$CD = \sqrt{\sum_k [y_{ki}/(\sum_k y_{ki}^2)^{1/2} - y_{kj}/(\sum_k y_{kj}^2)^{1/2}]^2}$$

where CD is the squared chord distance between two multivariate samples i and j, and y_{ki} is the abundance of the k-th species at site i (Jongman et al., 1995). Squared chord distance values can range from 0.0 to 2.0, with 0.0 indicating identical proportions of species within the samples being compared.

As cut-off value for 'good' analogues, the 5 % percentile of the closest analogues was chosen, the second decile (20 %) was chosen for describing 'poor analogues' (Birks, 1995). Similarity was calculated using the software MAT (Modern Analogue Technique) Version 1.1, written by Steve Juggins.

7.8 Mantel test

A Mantel's test evaluates the association between two distance matrices (Mantel, 1967; Legendre and Legendre, 1998). It was used to assess the correspondence between changes in the chironomid and diatom assemblages, e.g., if changes in both communities occur in a correlated pattern. Significance was tested using Monte Carlo randomisation with 999 iterations. The Mantel test was performed using the software PC-ORD Version 4.

Chapter V

Results

1 Core description and loss on ignition

From Lake Stora Kroksjön, four cores ca. 2 m long with an overlap of between 50 and 150 cm respectively were taken (see Table V.1 and Figure V.1). The cores covered a sediment depth of 357.5 cm. The lowermost core contained late-glacial clays in basal sequences. A gradual transition occurred from clays to clayey gyttja to gyttja. The upper cores consisted of soft uniformly black brown algal gyttja without macroscopic lamination.

From Lake Lilla Torkelsjön, three cores with an overlap of ca. 100 cm were retrieved. The cores covered a limnic sediment depth of ca. 340 cm below the sediment surface before reaching late-glacial sands, which were not included in the analyses. The limnic sediments consisted of soft uniformly black brown algal gyttja without macroscopic lamination. The cores at Stora Kroksjön were labelled SKR1 0-2m, SKR1 1-3m, SKR1 1.5-3.5m and SKR1 2-4m, those at Lilla Torkelsjön LTO1 0-2m, LTO1 1-3m and LTO1 2-4m.

The parallelisation of the core segments was performed visually by inspection of the LOI diagrams (Figure V.2 and Figure V.3) and henceforth were treated as one continuous sediment sequence. Differences in LOI values between the individual cores were generally very low, ranging around 2-3 %. In Lake Stora Kroksjön there were greater deviances in core SKR1 2-4m between 270 and 245 cm sediment depth. From this part of the core, no samples were analysed, but samples from SKR1 2-4m were only taken for analysis lower than 310 cm sediment depth, when LOI values matched those of SKR1 1.5-3.5. Lower and upper regions of SKR1 2-4m correlated well with the overlapping cores SKR1 1.5-3.5m and SKR1 1-3m. A detailed description of the LOI curves in context with the chironomid stratigraphy is given in Chapter V.3.

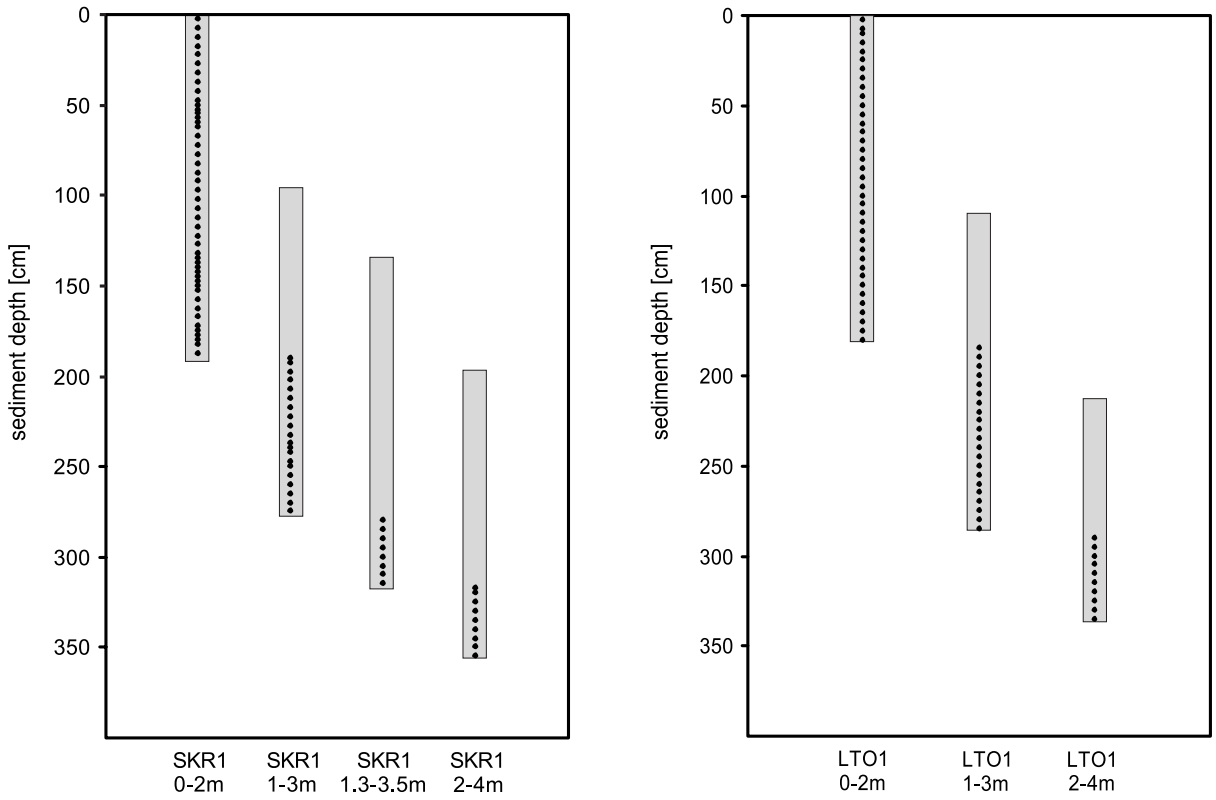
The intervals sampled for pollen, diatoms and chironomids (Figure V.1) were chosen to ensure that the Holocene sequence remained as undisturbed as possible. In Lake Stora Kroksjön, no samples were taken from the part of SKR1 2-4m (270-245 cm sediment depth) deviating in LOI, but exclusively from SKR1 1-3m (Figure V.1a). Three overlapping chironomid samples resulted in similar taxonomic proportions.

2 Dating

From each lake sediment sequence, six samples were dated by radiocarbon dating of terrestrial plant remains (leaves and bark) within the sediment (Table V.2). The age of the uppermost sample was estimated as 0. Sample ages were interpolated between the calibrated ^{14}C dates, assuming a linear sediment accumulation rate. The age-depth models are presented in Figure V.4.

Table V.1: Sediment description of the cores from Lakes Stora Kroksjön (SKR) and Lilla Torkelsjön (LTO)

Core	Sediment depth [cm]	absolute depth [cm]	description
SKR1 0-2m	0–187.5	0–187.5	brown to dark brown fine gyttja
	from 12.5 on		less water saturated
	from 27.5 on		fine detritus
SKR1 1-3m	0–176.5	95–271.5	dark brown fine gyttja
	176.5–185	271.5–280	clayey brown gyttja
SKR1 1.5-3.5m	0–107	135–242	brown to dark brown gyttja
	107–132	242–267	transition to clayey gyttja
	132–185	267–320	grey-greenish gyttja clay
SKR1 2-4m	0–55	185–240	dark brown gyttja
	55–85	240–270	transition to clayey gyttja
	85–132.5	270–317.5	grey-greenish gyttja clay
	132.5–172.5	317.5–357.5	grey clay
LTO1 0-2m	0–71	0–71	dark brown middle gyttja, high water content
	71–182	71–182	dark brown fine gyttja
LTO1 1-3m	0–177.5	110–287.5	dark brown fine gyttja with abundant detritus.
LTO1 2-4m	0–125	210–335	dark brown gyttja (fine detritus gyttja)
	125–148	335–357	clayey-silty fine sand, light gray, sharp transition
	148–185	357–397.5	medium sand



a. Stora Kroksjön b. Lilla Torkelsjön

Figure V.1: Overlap of the parallel cores taken in Lakes a) Stora Kroksjön and b) Lilla Torkelsjön. Dots are intervals sampled for chironomids, diatoms, and/or pollen.

2.1 Lake Stora Kroksjön

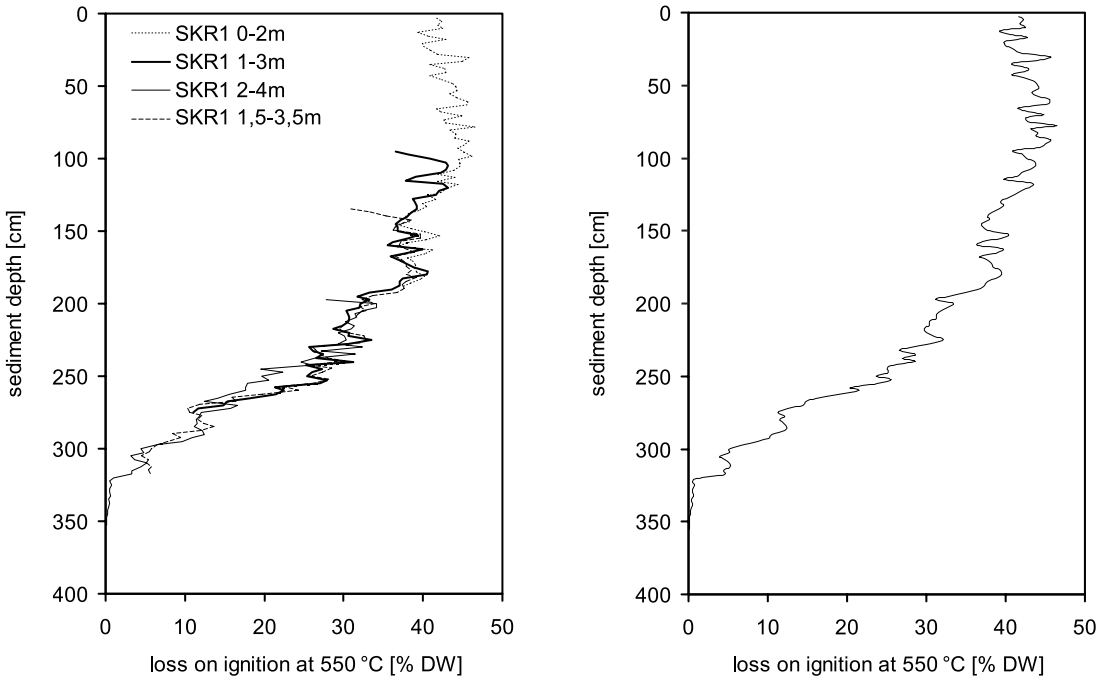
As the lowest dated horizon lay at 240 cm with an calibrated age of 9533 cal. yrs BP, ages for the samples between 240 to 355 cm depth were estimated by inspection of pollen diagrams and LOI curves (Figure V.5). Three estimates were integrated in the age-depth model:

1. the transition between the Younger Dryas and Preboreal chronozones (11,500 cal. yrs BP) was derived from comparing the pollen analysis to those of Berglund (1966a) and Björck (1979), and placed at 302.5 cm sediment depth. As stratigraphic markers, the rise in *Betula*, drop in *Pinus*, *Artemisia* and Chenopodiaceae pollen, and increasing LOI were used.

2. The isolation level from the Baltic Ice Lake was derived from the LOI curve and placed where organic carbon content started to rise over 0.5 % at ca. 14,000 cal. yrs BP (S. Björck, personal communication).

3. The lowest dates were calculated using a sedimentation rate of the relevant time interval (Older Dryas) at Farslycke, located near Lake Stora Kroksjön (Ising, 1998).

Depending on sediment depth, single samples (2.5 cm slices) encompassed between 78 to 132 years; sedimentation rate ranged from ca. 0.19 to 0.32 mm yr^{-1} and exhibited

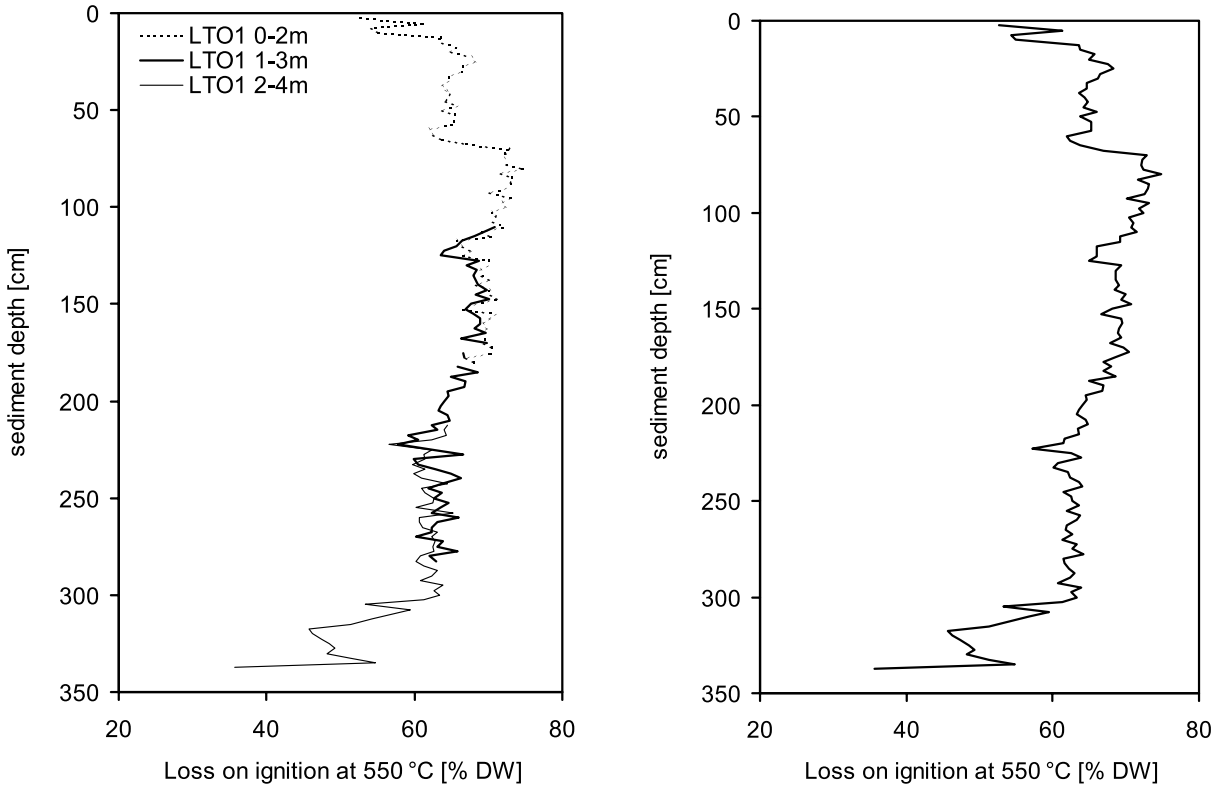


a. discrete cores b. cores merged to one sequence

Figure V.2: Loss on ignition at 550 °C at Lake Stora Kroksjön: values of the single cores are merged by forming mean values of all overlapping sequences; outlying values were ignored.

Table V.2: Radiocarbon dates of terrestrial material taken from Lakes Stora Kroksjön and Lilla Torkelsjön. Calibrated ages are given within 2 σ.

Lake	Sediment depth [cm]	sample size [mg]	Dates [^{14} C yr]	Calibrated age [cal. yrs BP]
Stora Kroksjön	47.5-50	50	1900 ± 95	2100-1550
	97.5-100	17	3465 ± 85	3930-3470
	137.5-140	40	4580 ± 85	5600-4950
	142.5-145	30	4790 ± 90	5710-5310
	187.5-190	12	6080 ± 90	7250-6650
	237.5-240	13	8590 ± 100	9950-9300
Lilla Torkelsjön	47.5-50	76	2100 ± 90	2360-1950
	97.5-100	65	3165 ± 90	3650-3050
	147.5-150	29	4230 ± 100	5050-4400
	197.5-200	38	5960 ± 90	7150-6550
	247.5-250	14	7480 ± 95	8420-8110
	305-307.5	12	8480 ± 100	9700-9100



a. discrete cores b. cores merged to one sequence

Figure V.3: Loss on ignition at 550 °C at Lake Lilla Torkelsjön: values of the single cores are merged by forming mean values of all overlapping sequences.

a near-linear relationship with depth (Figure V.4a). Below 240 cm depth, sedimentation rates calculated from the age estimates differed, ranging between 0.08 mm yr^{-1} and 4.8 mm yr^{-1} (estimate from Farslycke (Ising, 1998)). Therefore, single samples were calculated to cover long time periods during low sedimentation rates (313 years) and short periods during high sedimentation rates (6 years). The oldest date estimate was 14,068 cal. yrs BP.

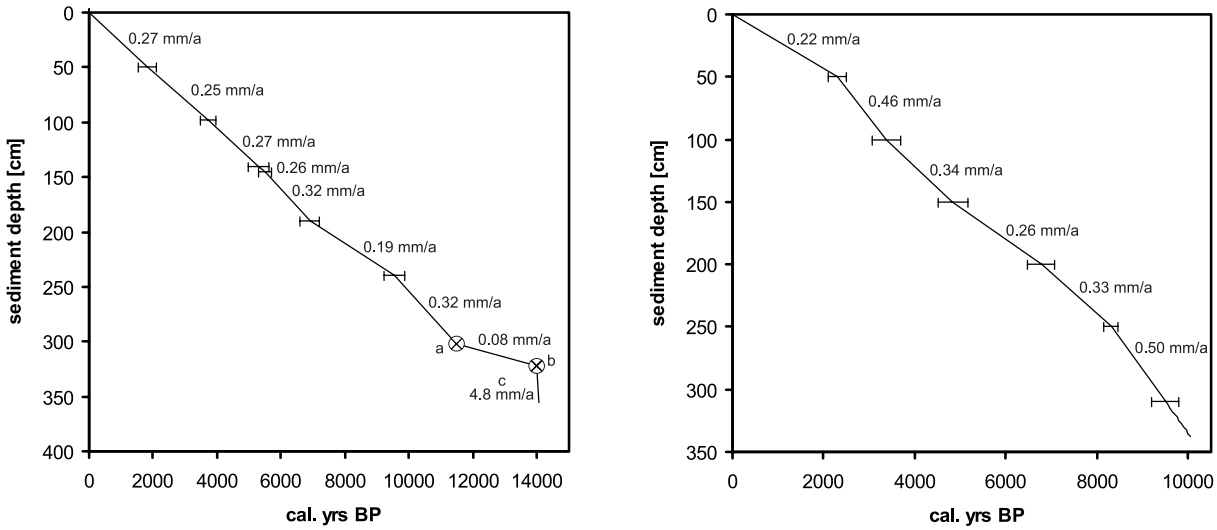
2.2 Lake Lilla Torkelsjön

The sandy sediments below 335 cm were not analysed and are not part of the age-depth model. Ages of the intervals lying below the lowermost dated horizon (312.5–335 cm) were extrapolated from the sedimentation rate calculated between the lowest two dates (Figure V.4b). The oldest age estimate for LTO was 10,003 cal. yrs BP. Sedimentation rates were highest in the lower part of the core (ca. 0.5 mm yr^{-1}) and lowest at the top (ca. 0.22 mm yr^{-1}). Single 2.5 cm slice samples encompassed between 50 and 115 years.

3 Chironomid analysis

3.1 Lake Stora Kroksjön

From the 44 samples analysed, 4187 chironomid head capsules were counted and assigned to 60 taxonomic groups. The lowermost sample analysed (325 cm depth) had



a. Stora Kroksjön b. Lilla Torkelsjön

Figure V.4: Age-depth models for Lakes a) Stora Kroksjön and b) Lilla Torkelsjön. Average sedimentation rates are calculated assuming linear accumulation rates between the calibrated radiocarbon dates. The lowermost two dates (Crossed circles) are estimates by comparison with pollen analysis and loss-on-ignition curve. a: GS-1/PB transition, ca. 11,500 cal. yrs BP; b: isolation level from BIL ca. 14,000 cal. yrs BP; c: sedimentation rate for the uppermost BIL sediments from a site in the vicinity (Ising, 1998).

only 23 head capsules picked from 50 cm^3 sediment. This sample was excluded from further analysis (see Chapter IV.4). The midge record is shown in Figure V.6.

The main feature of the chironomid stratigraphy was the predominance of the two taxa *Micropsectra insignilobus* gr. and *Sergentia coracina* during the Holocene. The chironomid stratigraphy, statistically divided into 2 significant zones following the broken stick model, was considered appropriate for further subdivision. The significant split lay at 207.5 cm depth between the zones SKR1-3 and SKR1-4 (7820 cal. yrs BP). The core is characterised by the following zones.

SKR1-1: 322.5–311.25 cm depth; 14,000–12,594 cal. yrs BP
Zone SKR1-1 was strongly dominated by *Micropsectra insignilobus* gr., making up between 30 and more than 60 % of the community. Other important taxa were *Microtendipes pedellus*, *Chironomus anthracinus* type, *Monodiamesa*, *Procladius*, *Protanypus*, and *Heterotrissocladius grimshawi*, and *H. maeaeri*.

SKR1-2: 311.25–292.5 cm depth; 12,594–11,185 cal. yrs BP
This zone showed a peak in *Heterotrissocladius grimshawi* close to 40 %, accompanied by a peak in *Stictochironomus* and comparatively high percentages of *Microtendipes*, *Procladius*, *Heterotrissocladius maeaeri*, and *Corynoneura scutellata*. *Micropsectra insignilobus* gr. was significantly less prominent than in the preceding zone, down to values between 20 and 10 % of the assemblage. *C. anthracinus* showed similar tendencies. *Sergentia coracina* occurred sporadically as single specimens. *Polypedilum*, which had been present in the preceding zone, was not present in three samples of this zone dated between 12,400–11,400 cal. yrs BP. *Tanytarsus lugens* type was found as single specimens twice in this zone.

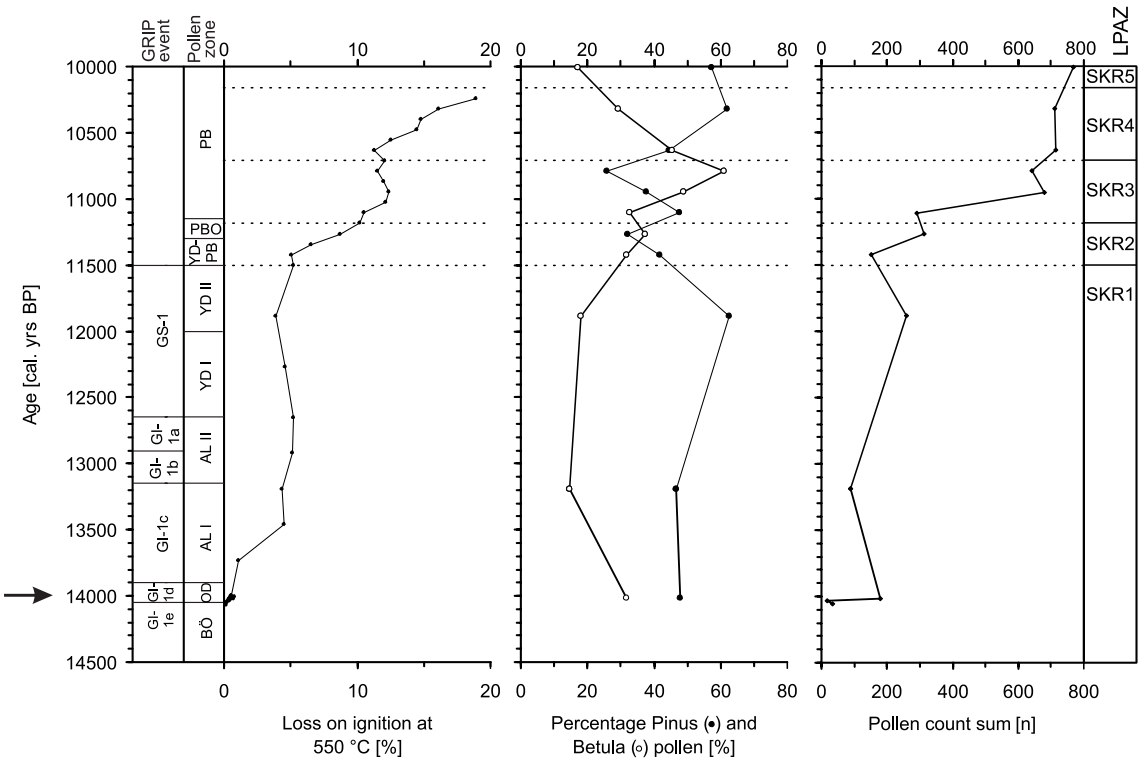


Figure V.5: Loss on ignition, *Pinus* and *Betula* pollen percentages and pollen count sums in the lowermost part of Lake Stora Kroksjön in relation to the GRIP event stratigraphy and pollen zones for southern Sweden. The arrow marks the point of isolation from the Baltic Ice Lake. BÖ = Bölling, OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PBO = Preboreal Oscillation, PB = Preboreal, GS, GI = Greenland Ice core record stadial and interstadial events. LPAZ = Local pollen assemblage zone, see Chapter V.5.1

SKR1-3: 292.5–207.5 cm depth; 11,185–7818 cal. yrs BP

In zone SKR1-3, *Micropsectra insignilobus* gr. dominated the assemblage. Other abundant taxa were *Dicrotendipes pulsus*, *Heterotrissocladius maeaeri*, and *Psectrocladius sordidellus* gr.. At the beginning of this zone, a diverse littoral chironomid fauna is established, represented by taxa as *Corynoneura scutellata*, *Limnophyes*, *Parakiefferiella bathophila*, *Ablabesmyia*, *Tanytarsus pallidicornis*-gr., *T. chinyensis*, *Dicrotendipes*, and *Lauterborniella agrayloides*. *Heterotanytarsus* appeared in the middle of the zone. *Procladius* abundance was less than in the preceding zones. *Monodiamesa*, which was present in the two first zones with between 3 and 5 %, disappeared in zone SKR1-3 at a level dated ca. 10,950 cal. yrs BP.

SKR1-4: 207.5–107.5 cm depth; 7818–4088 cal. yrs BP

SKR1-4 was marked by lower values of *Micropsectra insignilobus* gr., between 15–30 %. *Sergentia coracina* became the dominant taxon, increasing from 15 to 30 % by the end of the zone. Most of the other taxa remained within the same proportions of occurrence. *Chironomus anthracinus* was only found at two levels as single specimens and then disappeared completely from the assemblage. *Paratanytarsus penicillatus*, which had so far been a near-constant member of the species community, disappeared or was only found sporadically.

SKR1-5: 107.5–0 cm depth; 4088–0 cal. yrs BP

Sergentia coracina increased in abundance from 40 to 60 % in the middle of zone

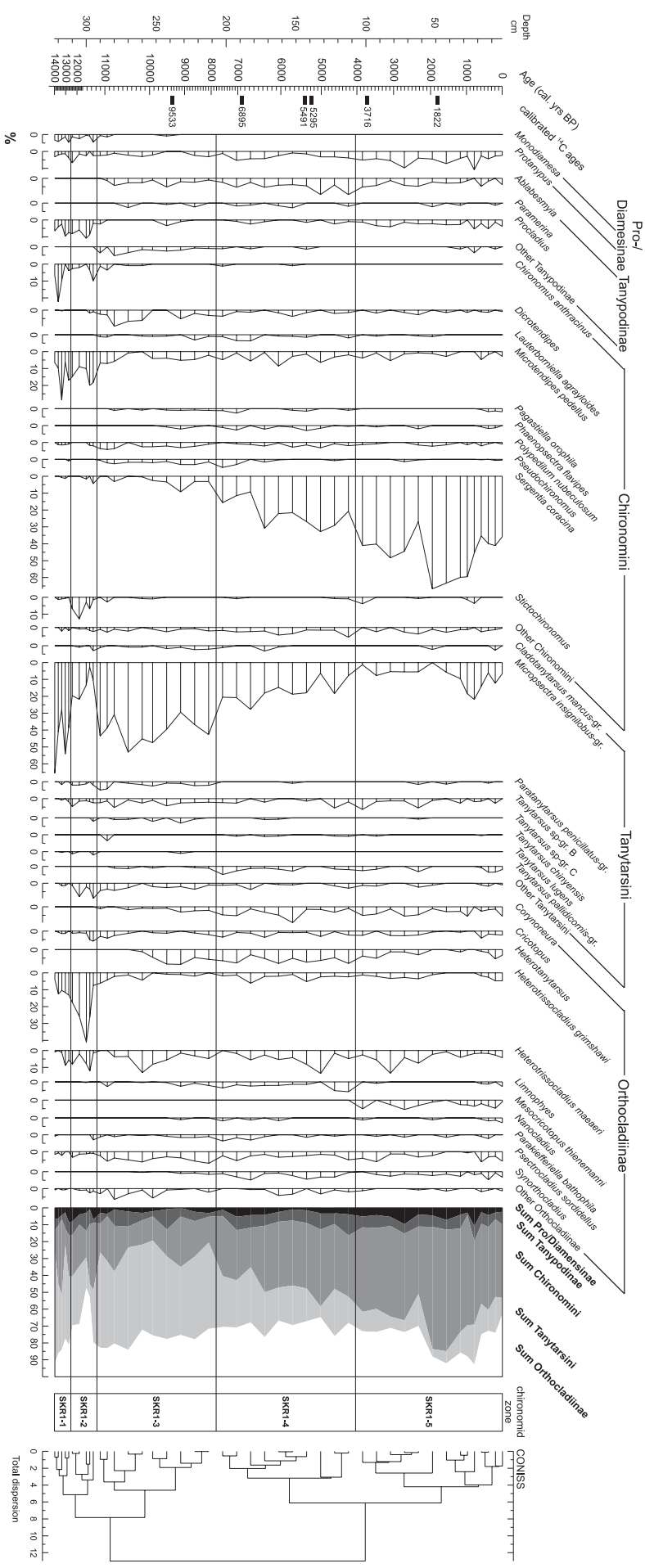


Figure V.6: Selected chironomid stratigraphy of Stora Kroksjön

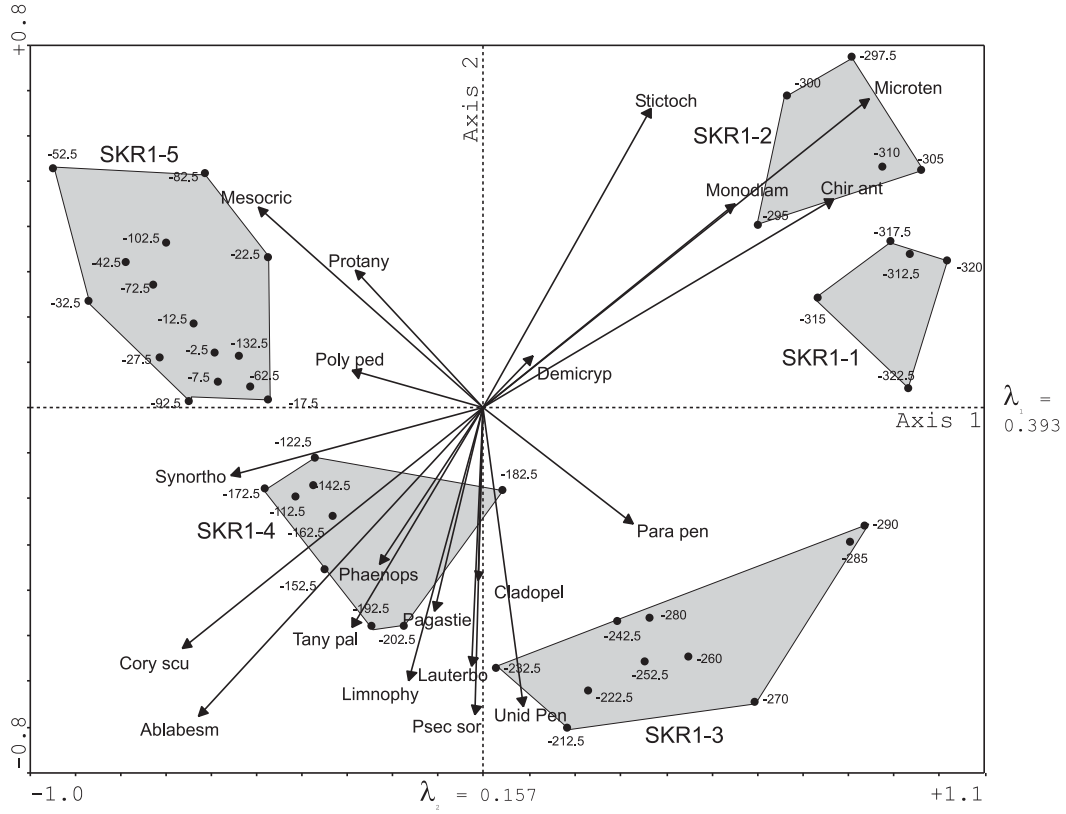


Figure V.7: PCA Ordination diagram of species scores (arrows) and sample scores forming an ecosystem trajectory for Lake Stora Kroksjön. Shaded areas encircle samples corresponding to the zones described in V.3.1. Minimum species fit was set to 20%. Abbreviations: Ablabesm = *Ablabesmyia*, Chir ant = *Chironomus anthracinus* type, Cladopel = *Cladopelma lateralis*, Cory scu = *Corynoneura scutellata*, Demicryp = *Demicryptochironomus*, Lauterbo = *Lauterborniella*, Limnophy = *Limnophyes*, Mesocric = *Mesocricotopus thienemanni*, Microten = *Microtendipes*, Monodiam = *Monodiamesa*, Pagastie = *Pagastiella*, Para pen = *Paratendipes penicillatus*-gr., Phaenops = *Phaenopsectra flavipes*, Poly ped = *Polypedilum pedellus*, Protany = *Protanypus*, Psec sor = *Psectrocladius sordidellus*-gr., Stictoch = *Stictochironomus*, Synortho = *Synorthocladius*, Tany pal = *Tanytarsus pallidicornis*, Unid Pen = unid. Pentaneurini

SKR1-5, while *Micropsectra insignilobus* gr. became less abundant with values less than 10 %, except for a single peak of 20 % at 25 cm depth (ca. 911 cal. yrs BP). *Mesocricotopus thienemanni* appeared as a new taxon and was found continuously until the top of the core. *Procladius* was again found continuously at less than 3 % of the assemblage.

Zonation and PCA

PCA (Figure V.7) revealed somewhat different patterns than the CONISS dendrogram (Figure V.6), as the method uses Euclidean distance as a dissimilarity index. SKR1-1 and SKR1-2 were visibly differentiated from the upper three zones by their species composition, characterised by e.g., *Chironomus anthracinus* type, *Stictochironomus*, *Monodiamesa*, and *Microtendipes pedellus*. The upper two zones were characterised by a variety of taxa, containing e.g., *Ablabesmyia*, *Corynoneura scutellata*, and *Mesocricotopus*. Axis 1 explained 39.3 % of the total variance in species data and axis 2 contributed 15.7 % of explained variance, adding up to 55 % explained variance within the chironomid data. The axes 3 and 4 added further 12.2 % explanation of

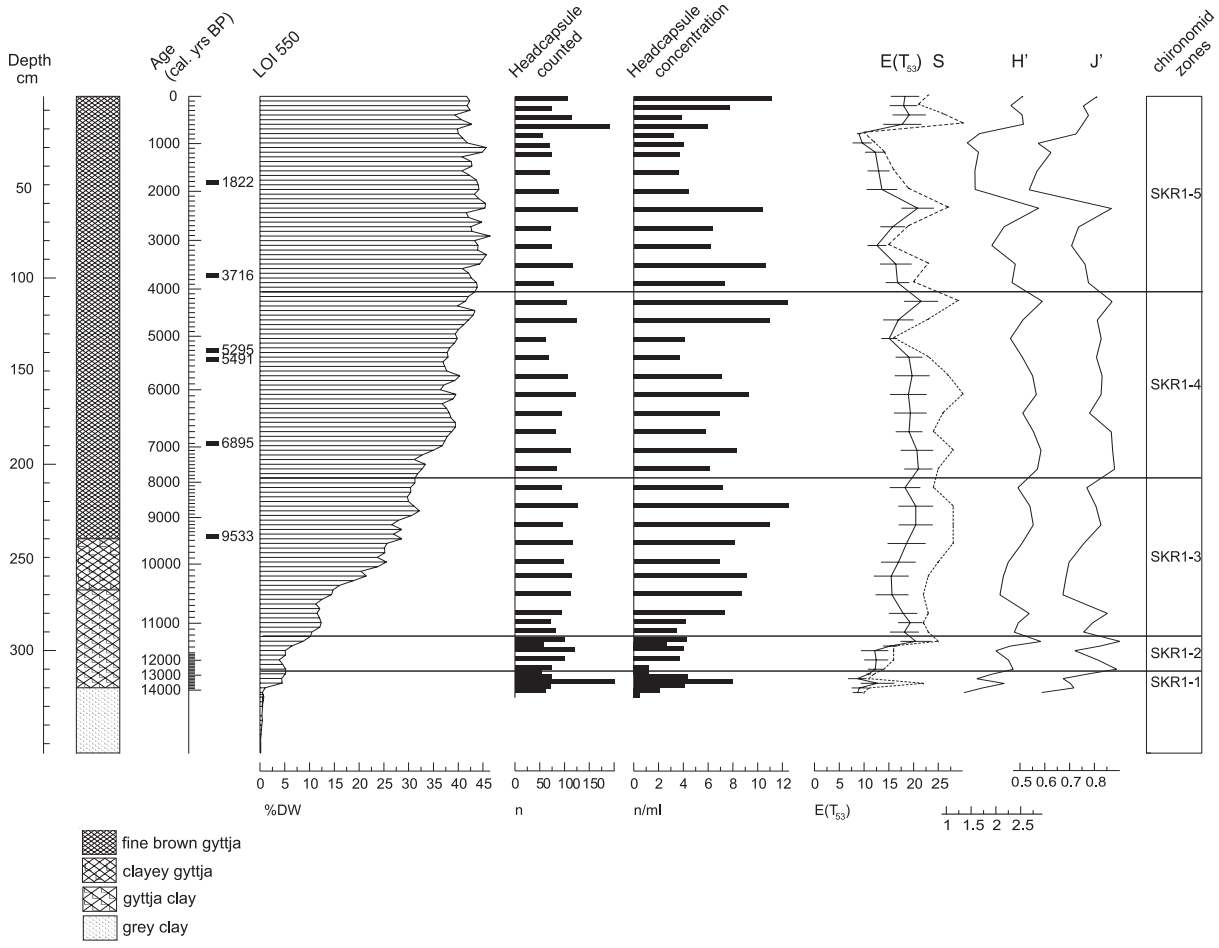


Figure V.8: Summary diagram of Stora Kroksjön's sediment characteristics and chironomid assemblage. Chironomid taxon richness (S, dashed line), rarefaction estimates ($E(T_{53})$ ±95 % confidence limits), diversity (H') and evenness (J') in the core. LOI: loss on ignition, DW: dry weight

the total variance in the data set. *Synorthocladius* was most closely related to the first ordination axis, whereas several taxa (*Psectrocladius sordidellus* gr., unidentified Pentaneurini, *Cladopelma lateralis*, and *Lauterborniella agrayloides*) were strongly related to the second axis.

The sample scores of PCA axis ranged between 0.5 and 1 from 14,000 to 10,300 cal. yrs BP, and decreased to negative values between 8000 and 7500 cal. yrs BP (Figure V.17a). An increasing negative trend occurred until ca. 1000 cal. yrs BP, where values reached about -1. PCA sample scores moved to about -0.5 by the top of the core.

Loss on ignition and chironomid biodiversity

A diagram of chironomid assemblage and sediment characteristics parameters is given in Figure V.8. In the grey clay at the bottom of the core, no chironomid head capsules were found. The first level with chironomid remains present (325 cm sediment depth) yielded only 23 head capsules and it was excluded from further analysis. The LOI values were less than 1 % in the clay and immediately increased in the transitional zone

when gyttja content in the sediment appeared. Head capsule concentration showed a distinct peak at the sample 317 cm. LOI remained around 5 % from 317 to 300 cm, where low values for chironomid species diversity and fluctuations in species evenness were also observed. From 300 cm depth onwards, LOI rose steadily to values around 40 % at 180 cm (ca. 6580 cal. yrs BP), where it remained stable until the top of the core. Loss on ignition was positively correlated with head capsule concentration ($r = 0.46$ at $p \leq 0.01$).

Species richness, diversity and evenness showed comparable patterns, fluctuating in the two lowermost zones, but being rather stable throughout a considerable part of the Holocene. In the uppermost zone, from ca. 4090 cal. yrs BP on (107.5 cm), all the indices fluctuated again, with a considerable drop in all indices after 2320 cal. yrs BP (62.5 cm).

3.2 Lake Lilla Torkelsjön

In the sediments of Lake Lilla Torkelsjön, 5382.5 head capsules were retrieved from 46 samples, and 5369 of them could be assigned to 61 taxonomic groups. The midge record could be divided into 3 significant zones (Figure V.9).

LTO1-1: 335–235 cm depth; 10,003–7846 cal. yrs BP

In zone LTO1-1, the most abundant taxa were *Tanytarsus* species-group B and *Ablabesmyia* (with average percentages of 12.5 and 13 %, respectively, *Chironomus anthracinus* type at 9 % and *Tanytarsus pallidicornis*-group with increasing values throughout the zone from about 5 to 10 %. Near the end of zone LTO1-1, *Einfeldia* and *Tanytarsus* species-group C decreased to values close to zero. *Chironomus anthracinus* type declined to values between 2.5 and 5 %. *Paratanytarsus penicillatus* was continually present with low values up to 270 cm, but occurred only as single specimens thereafter. Almost all other taxa in this zone occurred continuously throughout the zone in low percentages. *Corynocera ambigua* was present as single specimens at 335 and 317 cm. *Sergentia coracina* ranged between 0 and 12 %.

LTO1-2: 235–66.25 cm depth; 7846–2646 cal. yrs BP

Zone LTO1-2 was characterised by abundant *Tanytarsus* B and *T. pallidicornis* at 10 and 15 %, respectively. The first half of the zone was characterised by the near disappearance of *Einfeldia*, as well as declines in *Chironomus anthracinus* type and *Tanytarsus* C, and a slight increase in *Tanytarsus pallidicornis*-group, *Dicrotendipes pulsus*, and *Cladopelma lateralis*, relative to the preceding zone. *Ablabesmyia* decreased slightly to values of around 10 %, compared to zone LTO1-1. *Cladotanytarsus mancus* was slightly more abundant as was *Parakiefferiella bathophila*, compared to zone LTO1-1. *Glyptotendipes pallens*, *Omisus* and *Tanytarsus* C showed similar patterns of continuous, albeit low occurrence in the middle of the zone, between 180 and 100 cm. In the upper half of the zone, from 170 to 70 cm, *Phaenopsectra* and 'Chironomini larvulae' had peaks less than 10 and 5 %, respectively. *Sergentia* was near-absent from this zone.

LTO1-3: 66.25–0 cm depth; 2646–0 cal. yrs BP

This zone was marked by the abundance of *Heterotanytarsus*, *Psectrocladius septentrionalis*, *P. sordidellus* gr., and *Sergentia coracina*. *Tanytarsus lugens* type increased sharply in abundance, as did *Pagastiella*, relative to the preceding zone. *Ablabesmyia*, *Tanytarsus pallidicornis*-group and *Cladopelma lateralis* decreased in abundance compared to zone

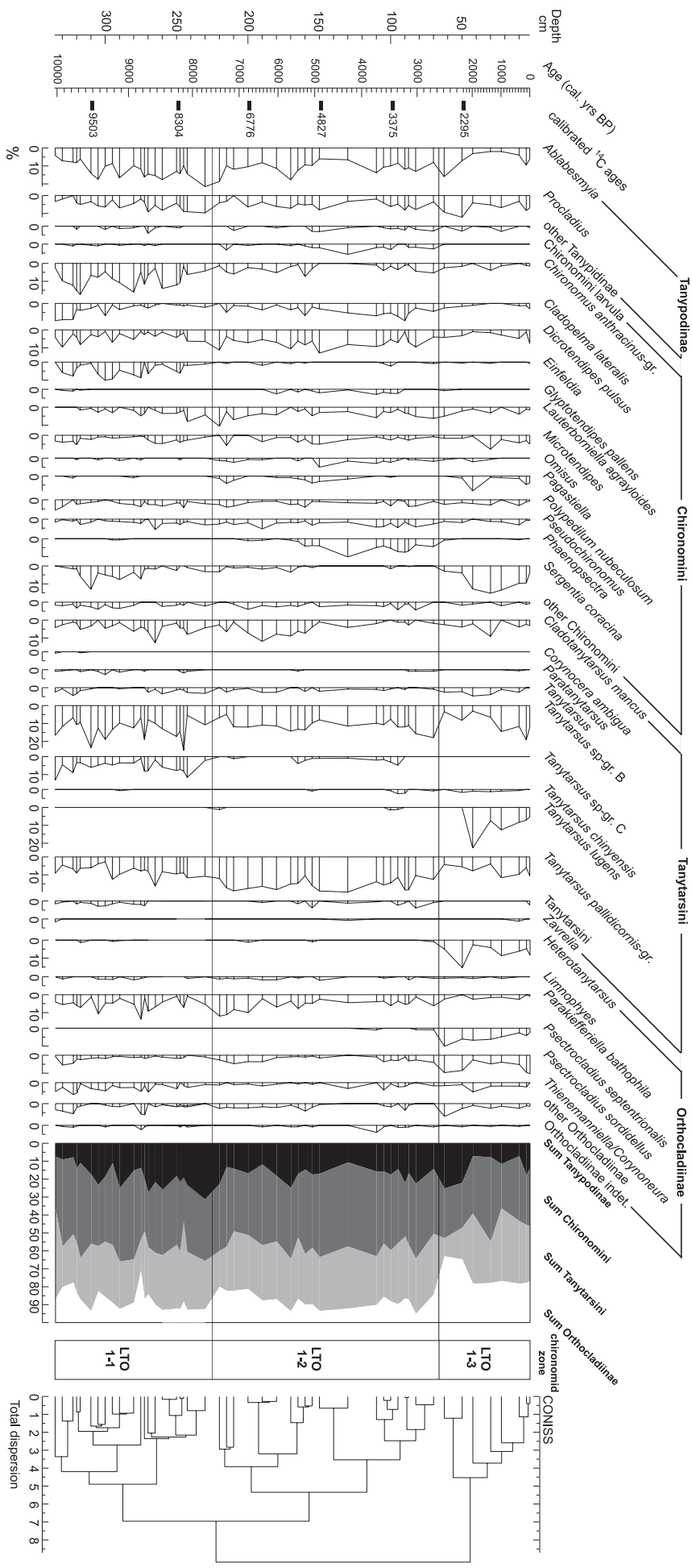


Figure V.9: Selected chironomid stratigraphy of Lake Lilla Torkelsjön

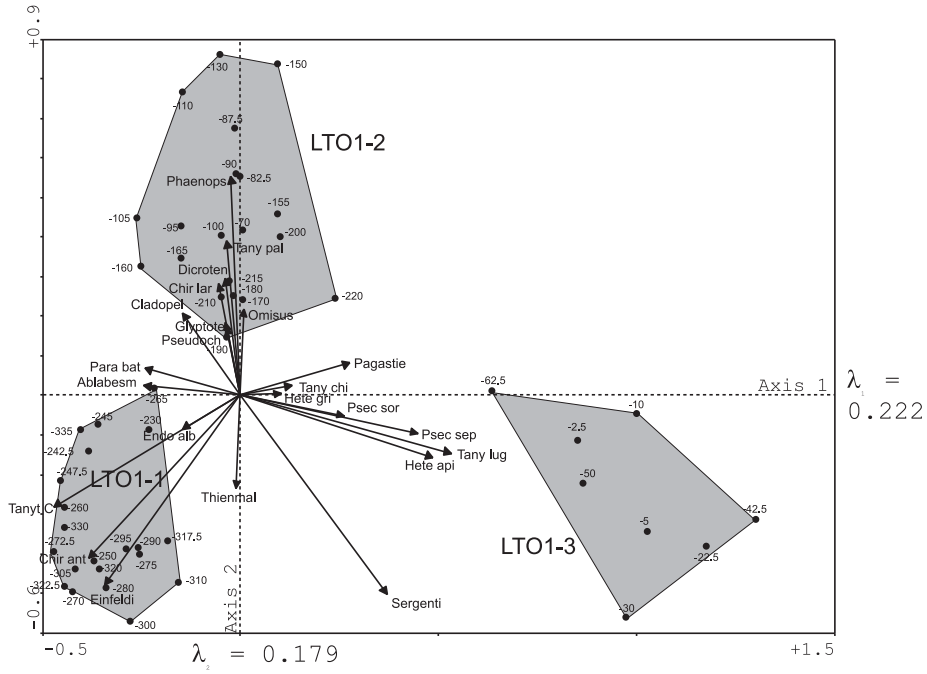


Figure V.10: PCA ordination diagram of species scores (arrows) and sample scores forming an ecosystem trajectory for Lake Lilla Torkelsj"on. Shaded areas encircle samples corresponding to the zones described in V.3.2. Minimum species fit was set to 20%. Abbreviations: Ablabesm = *Ablabesmyia*, Chir ant = *Chironomus anthracinus*-gr., Chir lar = Chironomini larvula, Cladopel = *Cladopelma lateralis*, Dicroten = *Dicrotendipes*, Einfeldi = *Einfeldia*, Endo alb = *Endochironomus albipennis*, Glyptote = *Glyptotendipes*, Hete api = *Heterotanytarsus apicalis*, Hete gri = *Heterotrissocladius grimshawi*, *Omisus*, Pagastie = *Pagastiella*, Para bat = *Parakiefferiella bathophila*, Phaenops = *Phaenopsectra*, Psec sep = *Psectrocladius septentrionalis*, Psec sor = *Psectrocladius sordidellus*-gr., Pseudoch = *Pseudochironomus*, Sergenti = *Sergentia coracina*, Tany C = *Tanytarsus* species-group C, Tany chi = *Tanytarsus chinyensis*, Tany lug = *Tanytarsus lugens* type , Tany pal = *Tanytarsus pallidicornis*-gr., Thienmal = *Thienemanniella*

LTO1-2, whereas *Tanytarsus chinyensis* was continually present in low percentages. The concentration of mandibles of the anoxia-tolerant dipteran *Chaoborus flavicans* increased greatly in the uppermost zone.

Zonation and PCA

PCA revealed similar patterns in respect of zonation and the most influential taxa differentiating the stratigraphical units (Figure V.10) as the CONISS. The first axis had an eigenvalue of 0.222, the second axis had an eigenvalue of 0.171, resulting in a cumulative percentage of explained variance in the species data of 39.3 %. The third and the fourth axes contributed 7.5 and 5.5 % variance explained, respectively. *Psectrocladius septentrionalis*, *Tanytarsus lugens* type and *Heterotrissocladius grimshawi*, characterizing the zone LTO1-3, were strongly positively associated with the first axis, and *Parakiefferiella bathophila* negatively covaried with axis 1. The second axis was predominantly associated with the taxa characterising zone LTO1-2, as e.g., *Tanytarsus pallidicornis*-group, *Phaenopsectra* and *Dicrotendipes*. These taxa are all typically found in the littoral zone of lakes. *Sergentia coracina*, a species typically found in the profundal of lakes, occurred predominantly in the zone LTO1-1 and LTO1-3 and contributed strongly to both axes.

PCA sample score had a value of -0.5 at 10,000 cal. yrs BP (Figure V.17b), and in-

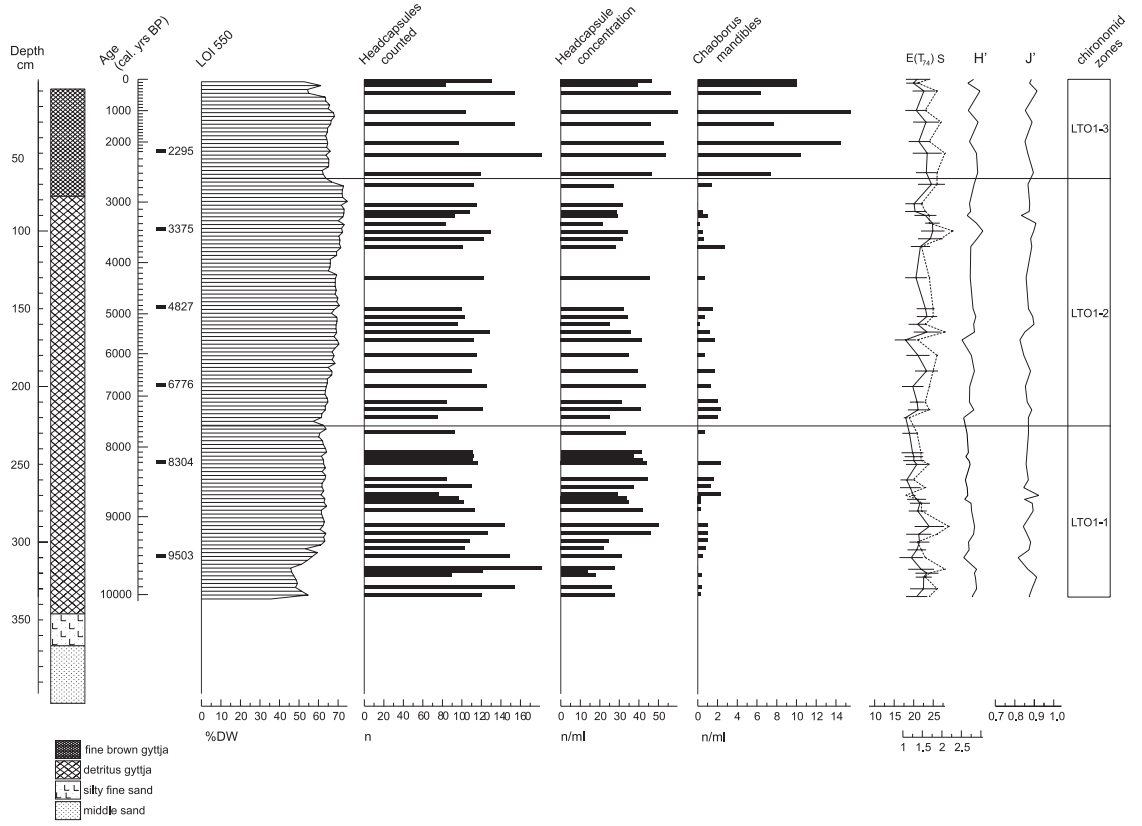
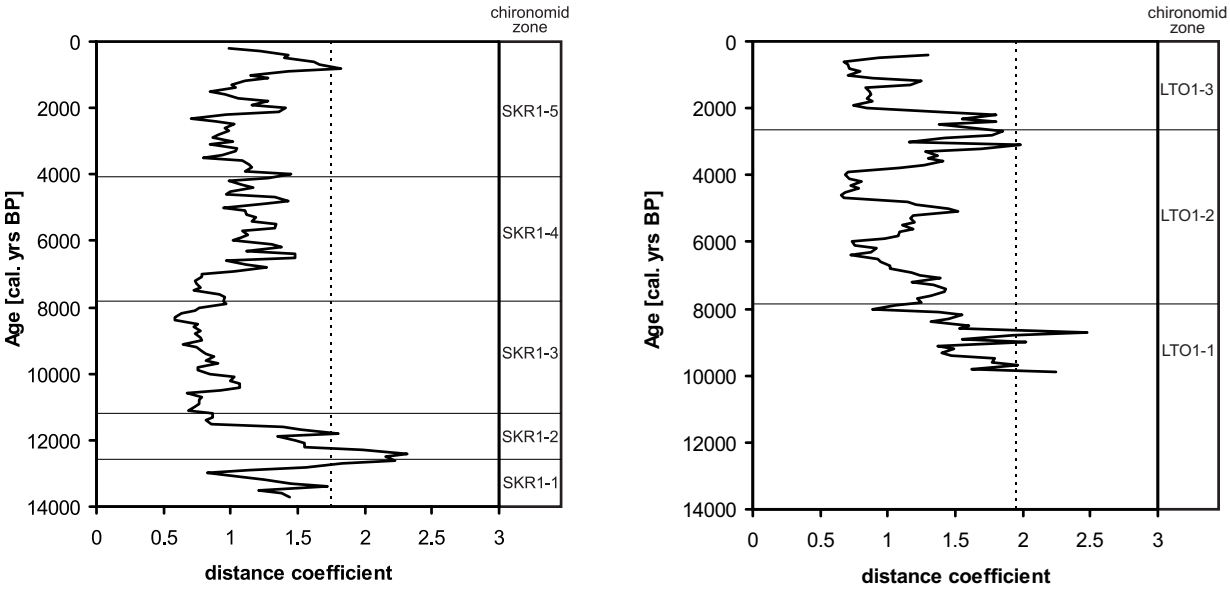


Figure V.11: Summary diagram of Lilla Torkelsjön's sediment characteristics, chaoborus mandible concentration and chironomid assemblage indices. Chironomid taxon richness (S, dashed line), rarefaction estimates ($E(T_{74})$ ±95 % confidence limits), diversity (H') and evenness (J') in the core. LOI: loss on ignition, DW: dry weight

creased to zero around 7600 cal. yrs BP. Until 2600 cal. yrs BP, values fluctuated between zero and -0.5. A large increase occurred after 2600 cal. yrs BP, to values > 1, and remained high to the present day.

Loss on ignition and chironomid biodiversity

LOI was already 40 % at 335 cm when the sediment consisted of gyttja. Values rose to 65 - 70 % and remained that high from 300 to 70 cm (ca. 9300–2600 cal. yrs BP). A drop of 8 % was observed at 70 cm, concurrent with the midge biostratigraphy boundary LTO1-2/LTO1-3, and values remained somewhat lower until the uppermost sample, relative to lower parts of the core (Figure V.11). Chironomid head capsule concentration ranged between 20 and 60 per ml and was thus considerably higher than in Lake Stora Kroksjön (Mann-Whitney U-test, $p < 0.0001$). It appeared to be uncorrelated to LOI except for in uppermost stratigraphical unit. Here, a distinct drop in LOI coincided with an increase in head capsule concentration in the uppermost zone. Species diversity and evenness showed consistently higher values with 2.76 and 0.87, respectively, than Lake Stora Kroksjön (Mann-Whitney U-test, $p < 0.0001$ in both cases). Species richness was not significantly different; the number of taxonomic groups was nearly identical (60 and 61). Fluctuation in all indices was low throughout the core.



a. rates of change SKR b. rates of change LTO

Figure V.12: Rates of chironomid community change (chord distance per 100 yr) in Lakes a) Stora Kroksjön (SKR) and b) Lilla Torkelsjön (LTO). Vertical dotted line represents 95% confidence limits based on Monte Carlo permutation tests with 5000 iterations.

3.3 Rates of chironomid community change

Rates of change in the chironomid community composition showed different patterns in the two lakes. At Lake Stora Kroksjön, rates of change attained significant ($p < 0.05$) values at two points. A conspicuous peak between 12,700 and 12,300 cal. yrs BP occurred at the boundary between zones SKR1-1 and SKR1-2 (Figure V.12a). Throughout the Holocene, the community remained stable, with rates of change values and fluctuation amplitude becoming significant once again at around 800 cal. yrs BP. In Lake Lilla Torkelsjön, two major periods with significant rates of change of the chironomid community could be discerned: in zone LTO1-1, there were two peaks at 9900 and 8700 cal. yrs BP, and a second period began ca. 3100 cal. yrs BP (Figure V.12b).

Rates of change at both sites from 10,000 until ca. 8000 cal. yrs BP differed significantly, with Lilla Torkelsjön showing distinctly higher rates of change. At Stora Kroksjön, the community was stable during this period. From 6000 until 4000 cal. yrs BP, rates of change showed low values at both sites. From 4000 to 2000 cal. yrs BP, values at Lilla Torkelsjön increased again, whereas those in Stora Kroksjön remained constant. Within the last 2000 years, values increased at Stora Kroksjön and have remained stable at Lilla Torkelsjön.

3.4 Mean July air temperature reconstruction

The Norwegian calibration model of chironomid-inferred air temperatures was applied to the fossil assemblages of Lakes Stora Kroksjön and Lilla Torkelsjön. Sample specific errors were estimated by Monte Carlo simulations with 500 iterations (Birks,

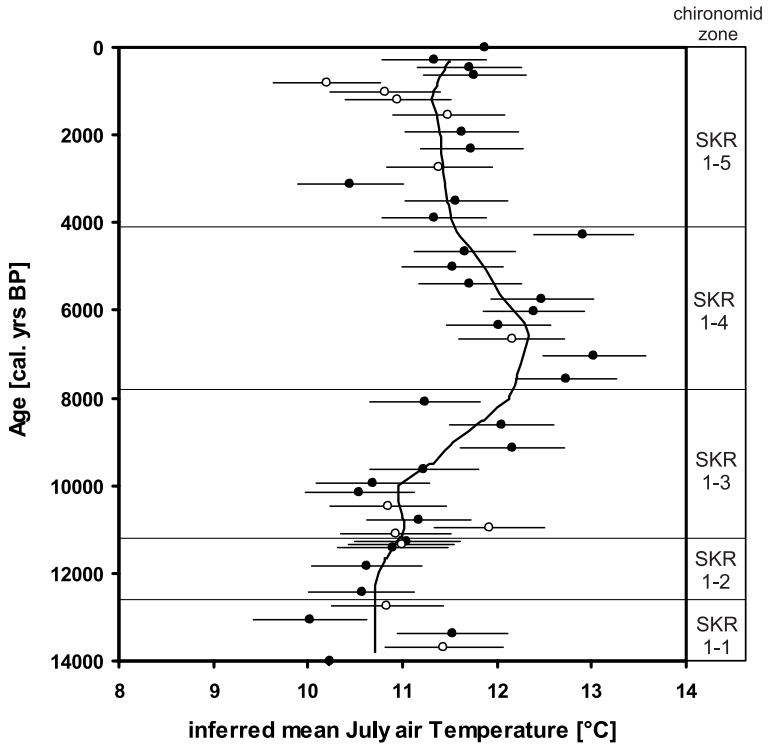


Figure V.13: Chironomid-inferred mean July air temperatures (°C) at Stora Kroksjön during the late Pleistocene and Holocene. Error bars are the sample specific prediction error. A LOWESS smoother (span = 0.25) has been superimposed on the inferred values. Open circles indicate no-analogue, filled circles poor analogue conditions.

1995). The RMSEP of the model amounts to 1.0119 °C (See Chapter IV.7.5).

Inferred summer temperatures at Lake Stora Kroksjön were generally low compared to today's temperature of 16.3 °C, with a minimum inferred temperature of 10 °C at 13,060 cal. yrs BP (315 cm) and a maximum inferred temperature of 13 °C at 7027 cal. yrs BP (192,5 cm) (Figure V.13). The sample-specific errors ranged from 1.05 to 1.3 with a mean of 1.13 °C. Until ca. 9600 cal. yrs BP, temperatures generally remained below 11 °C. From there until ca. 4300 cal. yrs BP, temperatures were higher, up to 13 °C. There was a distinct drop to 11.2 °C at 8080 cal. yrs BP (212,5 cm). From 4300 until ca. 820 cal. yrs BP, a general decreasing trend occurred. Reconstructed temperatures rose up to between 11 and 12 °C in the uppermost 4 samples. The sample representing present-day conditions inferred a temperature of 11.8 °C.

A detailed graph of the Late-glacial/Holocene transition (Figure V.14) reveals a distinct warming trend within the first part of the Allerød, then a drop to 10 °C at 13,050 cal. yrs BP. the next sample in the Allerød period inferred warmer conditions, then during Younger Dryas, temperatures decreased slightly. Towards the onset of the Holocene, temperatures started to rise, showing one small drop around the time of the Preboreal oscillation (PBO, 11,300 to 11,150 cal. yrs BP) and one markedly warm sample at 10,900 cal. yrs BP. During the Preboreal, inferred temperatures remained low and only started rising distinctly around 9600 cal. yrs BP.

At Lake Lilla Torkelsjön, chironomid-inferred summer air temperatures ranged

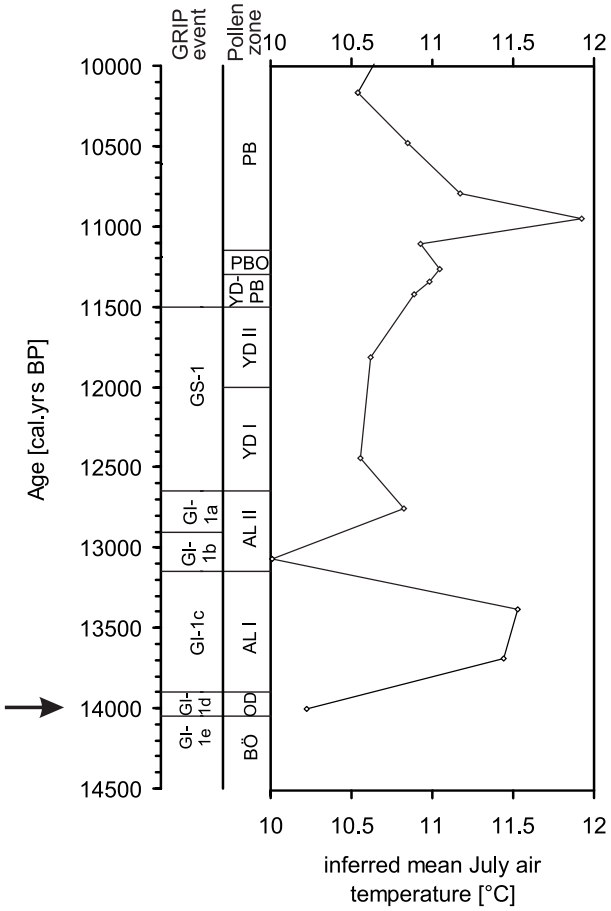


Figure V.14: Chironomid-inferred summer air temperatures at Stora Kroksjön during the late-glacial/Holocene transition. The arrow marks the point of isolation from the Baltic Ice Lake. BÖ = Bölling, OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PBO = Preboreal Oscillation, PB = Preboreal, GS, GI = Greenland Ice core record stadial and interstadial events .

between 10.7 and 15.3 °C (Figure V.15). The sample-specific prediction errors ranged from 1.04 to 1.33 with a mean of 1.10 °C. From the core bottom until ca. 5000 cal. yrs BP, temperatures fluctuated around 13 °C, with occasional inferred values around 12 °C, e.g., at 9300 (300 cm), 8700 (270 cm) and 8150 cal. yrs BP (245 cm), though three samples inferred temperatures higher than 14 °C. Between 5000 and 2500 cal. yrs BP, the inferred temperatures rose markedly, up to 15.3 °C. From 2500 cal. yrs BP (zone boundary LTO1-2/LTO1-3) until the top of the core, inferred temperatures decreased to around 11.5 °C, below the values at the bottom of the core. For the topmost sample, representing modern conditions, 11.8°C was inferred.

Inferred temperatures at Lake Lilla Torkelsjön were generally warmer than those of Lake Stora Kroksjön. Putting both sites in the same time frame (Figure V.16), it is apparent that temperature trends show similarities, except for the time period between 5000 and 2300 cal. yrs BP. Here, differences of as much as 4 °C were observed. At both sites, a drop in inferred temperature of about 1 °C was recorded around 8200 cal. yrs BP. The two uppermost samples infer near-identical values (11.8 °C). Present day mean July air temperature av-

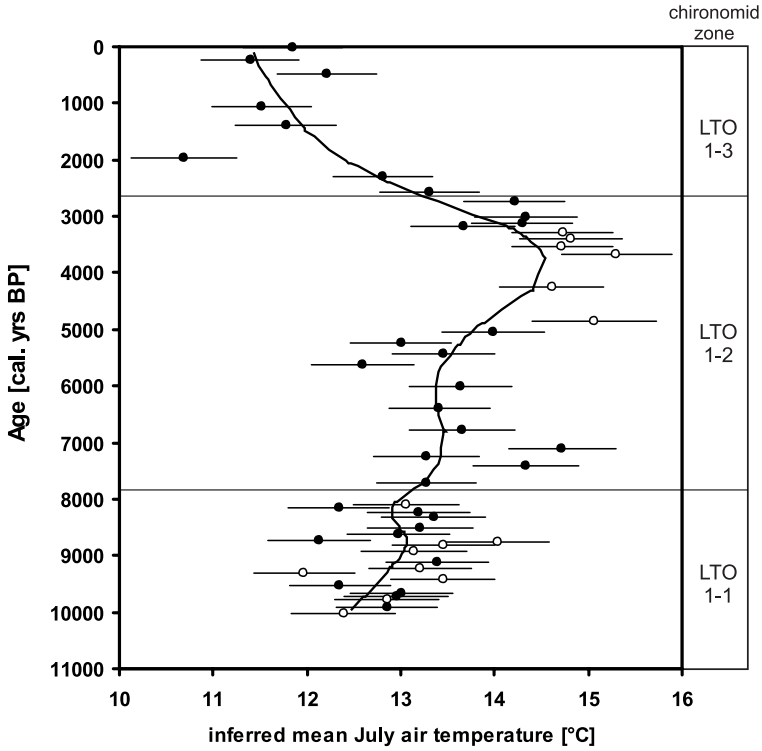


Figure V.15: Chironomid-inferred mean July air temperatures (°C) at Lilla Torkelsjön during the Holocene. Error bars are the sample specific prediction error. A LOWESS smoother (span = 0.25) has been superimposed on the inferred values. Open circles indicate poor analogue, filled circles good analogue conditions.

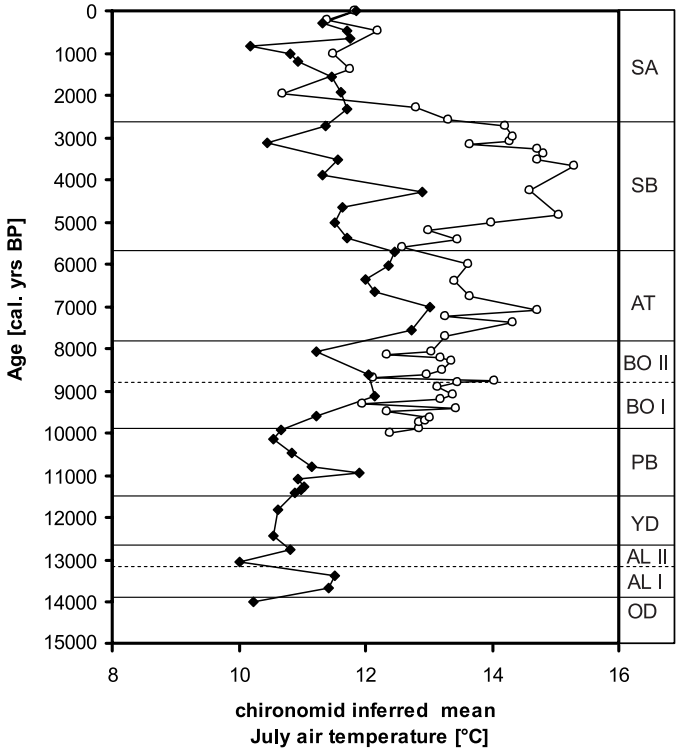
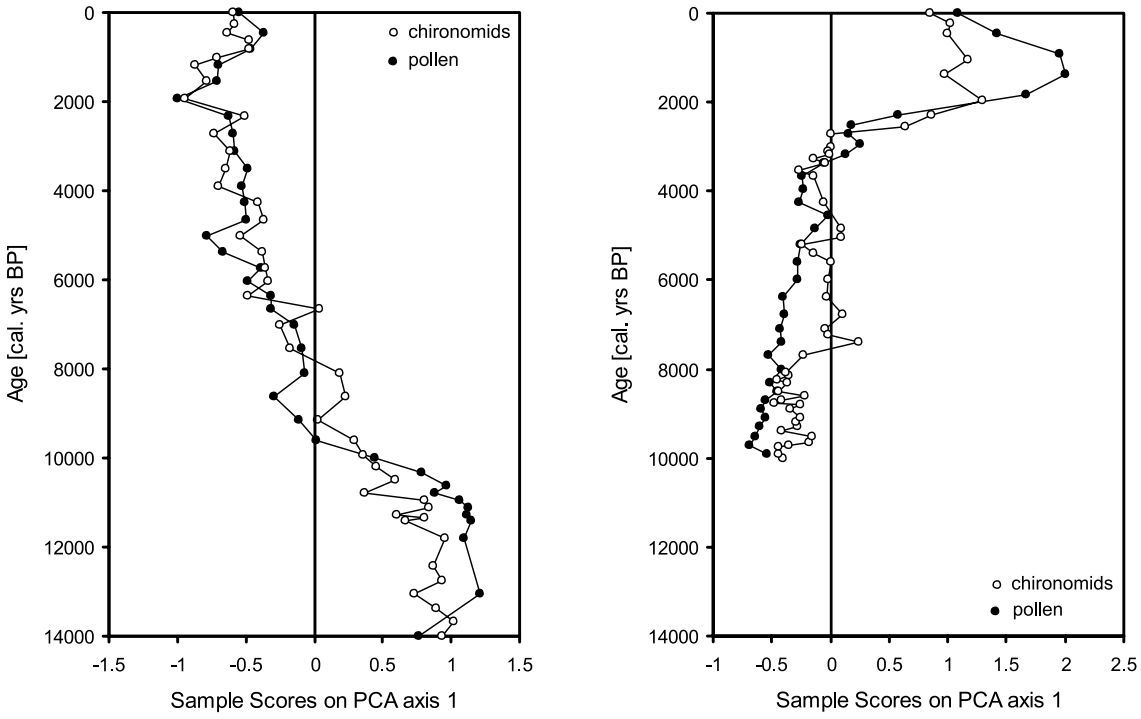


Figure V.16: Chironomid-inferred mean July air temperatures at Lakes Stora Kroksjön (diamonds) and Lilla Torkelsjön (open circles) in comparison. Abbreviations: OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PB = Preboreal, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum.



a. sample scores at SKR b. sample scores at LTO

Figure V.17: Stratigraphic plots of pollen and chironomid PCA axis 1 sample scores at a) Lake Stora Kroksjön (pollen: $\lambda_1 = 0.463$, chironomids: $\lambda_1 = 0.393$) and b) Lake Lilla Torkelsjön (pollen: $\lambda_1 = 0.554$, chironomids: $\lambda_1 = 0.222$)

eraged over the last 30 years is 16.3 °C, measured at a weather station in the vicinity of the sites.

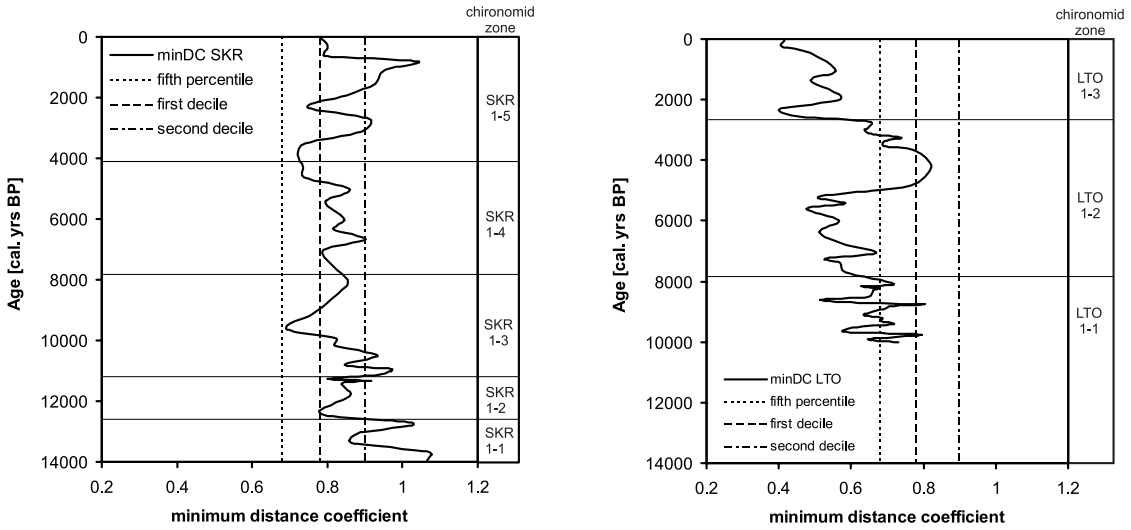
3.5 Modern analogues

One means of assessing the reliability of the temperature reconstruction is to analyse the taxonomic overlap of fossil data with the modern calibration set. Presence or absence of taxa, as well as species abundances, at a given site are considered in the analysis.

At Lake Stora Kroksjön, of the 60 taxa present in the fossil assemblage, 59 occurred in the calibration set. The only species not present in the calibration set was *Conchapelopia*, which only represented 0.12 % of the total fossil assemblage. At Lilla Torkelsjön, 60 of the 61 fossil taxa were represented in the calibration set: Here, the missing taxon *Einfeldia* comprised 2.2 % of the total fossil assemblage.

To assess the assemblage similarity, the 5^{th} percentile of the distances in the calibration data set was used as the upper value for a good analogue situation, 20 % as upper threshold for poor analogue situation (Birks, 1995). Chord distance was used as a distance coefficient.

Overlap with the modern Norwegian chironomid data set differed between the two lakes (Figure V.18a and Figure V.18b). From Lake Stora Kroksjön, most of the samples lay below the 20 % threshold value of poor analogue situation. Some samples, however, showed higher values, especially in the time between 1549 and



a. Minimum DCs at SKR b. Minimum DCs at LTO

Figure V.18: Minimum dissimilarity coefficients (min DCs) in a) Stora Kroksjön (SKR) and b) Lilla Torkelsjön (LTO). Percentile thresholds given mark thresholds for good (5 %) and poor analogue (20 %) situations

820 cal. yrs BP (42.5 to 22.5 cm) and prior to 10,480 cal. yrs BP (270 cm). These samples coincided quite regularly, though not exclusively, with low total number of head capsules counted (below 80 head capsules). The correlation between minimum dissimilarity coefficient and total count was highly significant (p=0.0006). The overall analogue situation at Stora Kroksjön was poor, as no value lay below the 5% percentile.

In Lake Lilla Torkelsjön, most of the samples showed minimum dissimilarity coefficient values (DCs) below the 5 % percentile threshold and can therefore be described as having good analogues within the calibration data set (Figure V.18b). However, in the section from 4830 until 3160 cal. yrs BP (corresponding to 150 to 90 cm) and at the bottom of the core, several minimum dissimilarity coefficient (DC) values lay above the 5 % threshold value of 0.679. These latter were all samples with a high occurrence of *Einfeldia*.

4 Diatom analysis

In both lakes, high numbers of diatom species were found; 344 taxa could be distinguished in Stora Kroksjön and 286 taxa in Lilla Torkelsjön. As many taxa only occurred in very low proportions, a reduction of taxa was necessary for statistical purposes. All taxa not reaching at least 0.5 % occurrence in one sample were excluded from further analysis. In each analysed sample, more than 300 diatom valves were counted.

4.1 Lake Stora Kroksjön

In Stora Kroksjön, 52 samples were analysed for diatoms. Samples 355, 345, and 335 cm contained less than 200 valves and were therefore excluded from further analysis; thus, the diatom record starts at 325 cm. In the remaining 49 samples, 344 taxa were distinguished. 150 taxa reached values of $\geq$ 0.5 % and were included in further analysis. Of these, for the reason of graphical

clearness, only the 41 taxa with a proportion of more than 2.5 % in at least one sample are presented in Figure V.19. The assemblage was divided into 4 significant zones.

SKRdia-1: 325–255 cm depth; 14,035–10,005 cal. yrs BP
Zone SKRdia-1 was characterised by the continuous low proportion occurrence of *Brachysira zellensis*, *Calvinula jaernefelti*, *Fragilaria construens* var. *venter*, *F. martyi*, *F. pinnata*, *Gomphonema coronatum*, and *Tabellaria flocculosa*, and by peak occurrences of *Aulacoseira 'pseudoislandica'*, *Cyclotella pseudocomensis*, *Fragilaria lapponica*, and *Navicula aboensis*. Benthic diatoms such as *Amphora fogediana, Brachysira neoexilis, Cavinula jaernefelti, Fragilaria exigua, F. martyi, F. pinnata*, and *Navicula aboensis* were present in abundance.

SKRdia-2: 255–236.25 cm depth; 10,005–9335 cal. yrs BP
From the beginning of the zone, ca. 10,000 cal. yrs BP, indifferent and planktonic taxa dominated the assemblage. The dominance of *Cyclotella tripartita* is the main feature of this zone. In two samples, this taxon had proportions of 46 and 53 %, respectively. Many of the diatoms present in zone 1 were absent here, such as *Fragilaria pinnata*, *Navicula aboensis*, and *Tabellaria flocculosa*.

SKRdia-3: 236.25–117.5 cm depth; 9335–4459 cal. yrs BP
Cyclotella pseudocomensis and *Aulacoseira 'pseudodistans'* increase at the beginning of this zone to between 30 and 50 % and around 25 %, respectively. *Cyclotella radiosa* was present at 16 % in the first half of this zone, decreasing to an average of 5 % in the latter half. *Cyclotella tripartita*, which had been abundant in the preceding zone, was almost completely absent from this zone. The taxon *C. krammeri* completely disappeared from the stratigraphy towards the zone end, whereas *C. stelligeroides* and *Fragilaria nanana* increased in the upper half of the zone. *C. rossii* is present in three continuous samples in the lower half of the zone.

SKRdia-4: 117.5–0 cm depth; 4459–0 cal. yrs BP
In this zone, *Aulacoseira 'pseudodistans'* was the dominant species, occurring between 20 and 40 %. *Cyclotella pseudocomensis* was not present in this zone, whereas *C. tripartita* reappeared and remained present throughout the zone at about 15 %. *Aulacoseira alpigena* and *Tabellaria flocculosa* had slightly higher percentages than in the previous zone.

Species richness and community diversity

CONISS cluster analysis (Figure V.19) showed that the species assemblage was divided into three distinct communities. Until ca. 9330 cal. yrs BP, comprising zones SKRdia-1 and SKRdia-2, species assemblages showed quite high dissimilarities. Dominance-fluctuations between benthic and planktonic species occurred frequently. During the mid- and late Holocene (zones SKRdia-3 and SKRdia-4), species assemblages were similar among within-zone samples, though distinguished by the presence or absence of *Cyclotella pseudocomensis* and *C. tripartita*.

The number of determined species (single-valve counts excluded) was high in the early parts of the stratigraphy (with the exception of the oldest sample yielding enough valves for statistical analysis) and decreased somewhat during the Early Boreal, between 10,000 and 9000 cal. yrs BP (Figure V.20a). Highest species numbers were recorded in the samples from 12,440 (64 species) and 11,110 cal. yrs BP (71 species). The num-

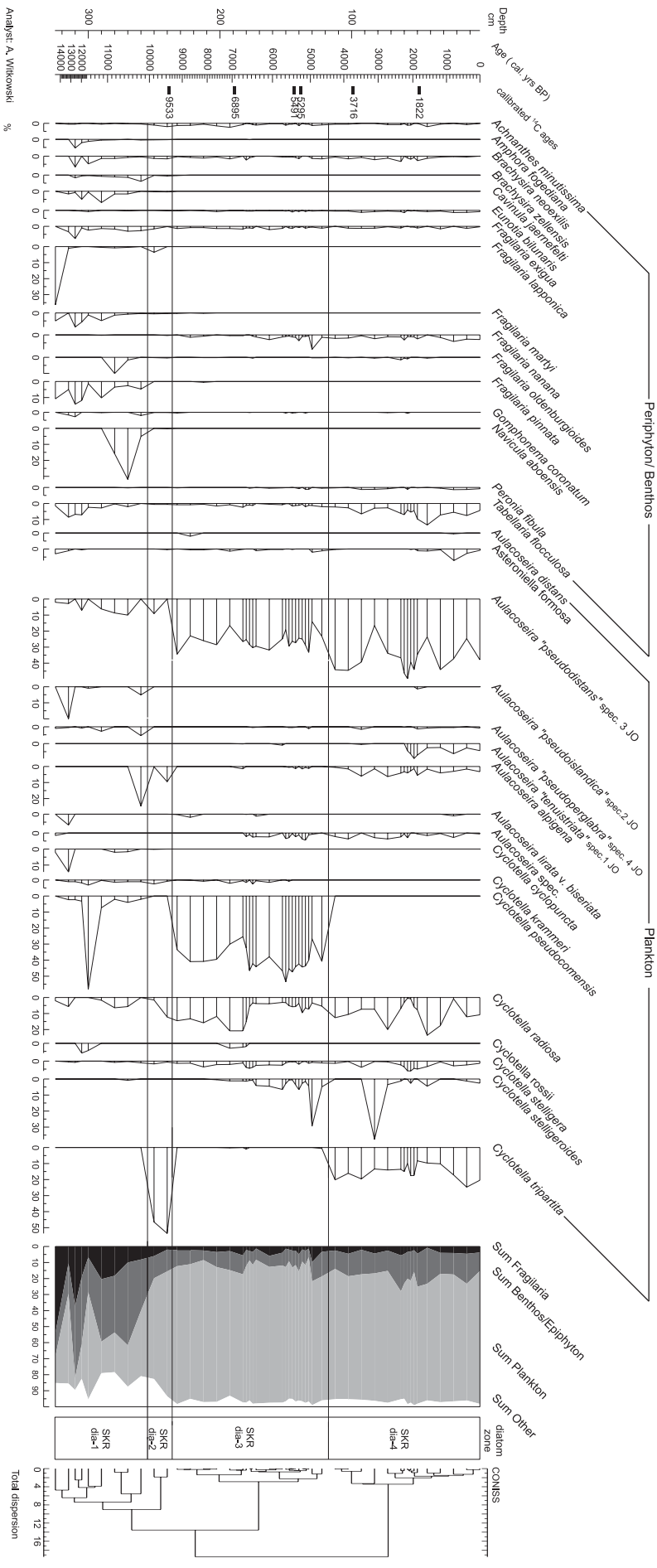
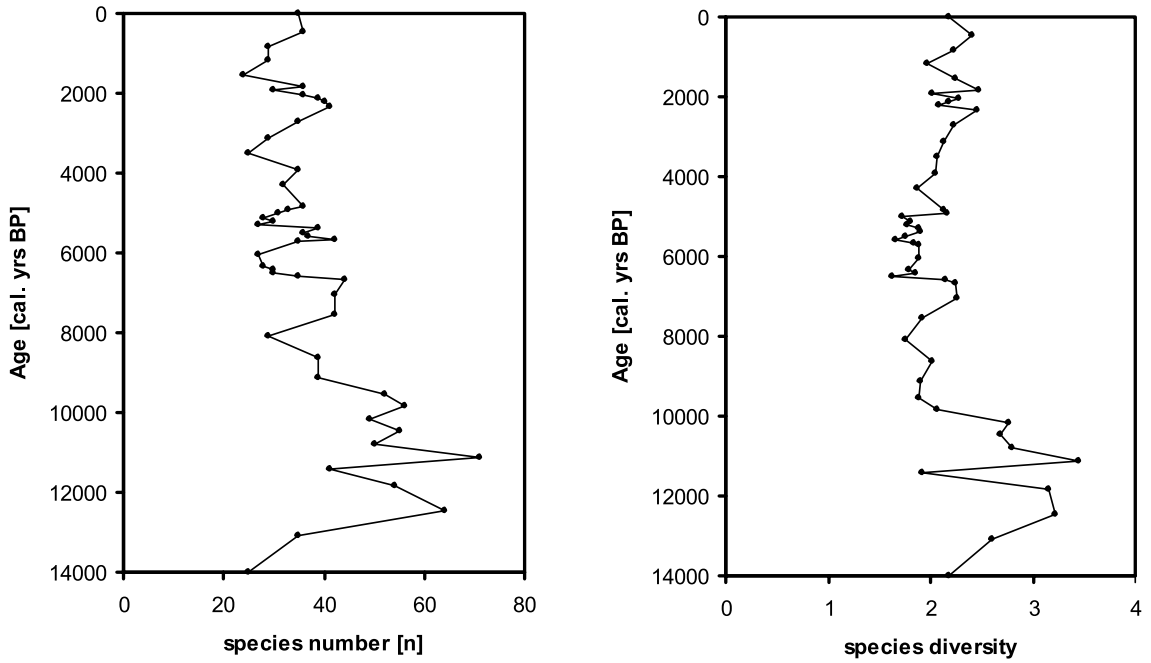


Figure V.19: Percent abundance of abundant diatom taxa at Lake Stora Kroksjön. The sums include taxa not shown in detail. JO: Lake Julma Ölkky, species sensu Lange-Bertalot and Metzelin (1996)



a. diatom species numbers b. diatom species diversity

Figure V.20: Species numbers and Shannon-Weaver species diversity index of diatoms at Lake Stora Kroksjön

ber of species found in samples younger than 9100 years was considerably lower and averaged around 34.

Species diversity was highest during the late-Pleistocene part of the core, but punctuated by one low value at 11,400 cal. yrs BP (Figure V.20b). From ca. 9500 cal. yrs BP on (nearly concurrent with the start of zone SKRdia-3) until the top of the core, species diversity values became stable with values around 2.

4.2 Lake Lilla Torkelsjön

In Lilla Torkelsjön, 35 samples were analysed for diatoms and 286 taxa were distinguished. From these, 195 were included in the statistical analysis, having percentages of ≥ 0.5 % in at least one sample. The assemblage was divided into four significant stratigraphical sections (Figure V.21).

LTOdia-1: 335–245 cm depth; 10,003–8151 cal. yrs BP
This zone is characterised by *Cyclotella stelligeroides* which is abundant in the middle of the zone at nearly 70 %. The latter part of the zone is characterised by a peak in *C. stelligera* at 65 %. Other important diatoms include approximately 5 to 10 % *Fragilaria gracilis*, and peaks of *Fragilaria nanana*, *Tabellaria flocculosa*, *Aulacoseira 'pseudodistans'*, *A. 'pseudoislandica'*, and *Cyclotella cyclopuncta*.

LTOdia-2: 245–135 cm depth; 8151–4391 cal. yrs BP
This zone was dominated by *C. stelligeroides*, which accounted for between 40-65 % of the valves counted. Other important taxa were *Fragilaria gracilis* and *Brachysira brebissonii*. *C. stelligera*, which occurred at > 60 % in the previous zone, decreased to values < 5 % and disappeared from the assemblage by the middle of the zone. Several benthic species appeared, such as *Brachysira*

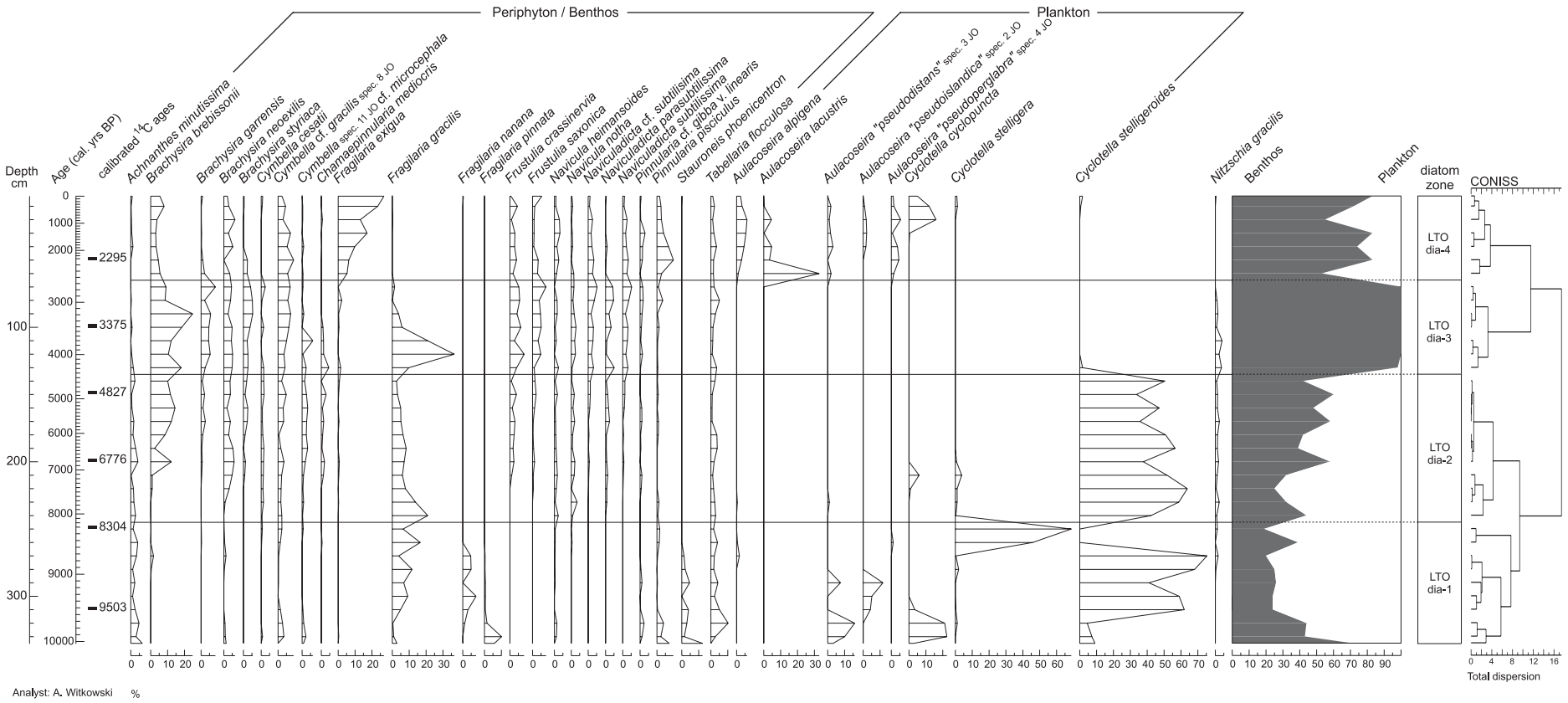
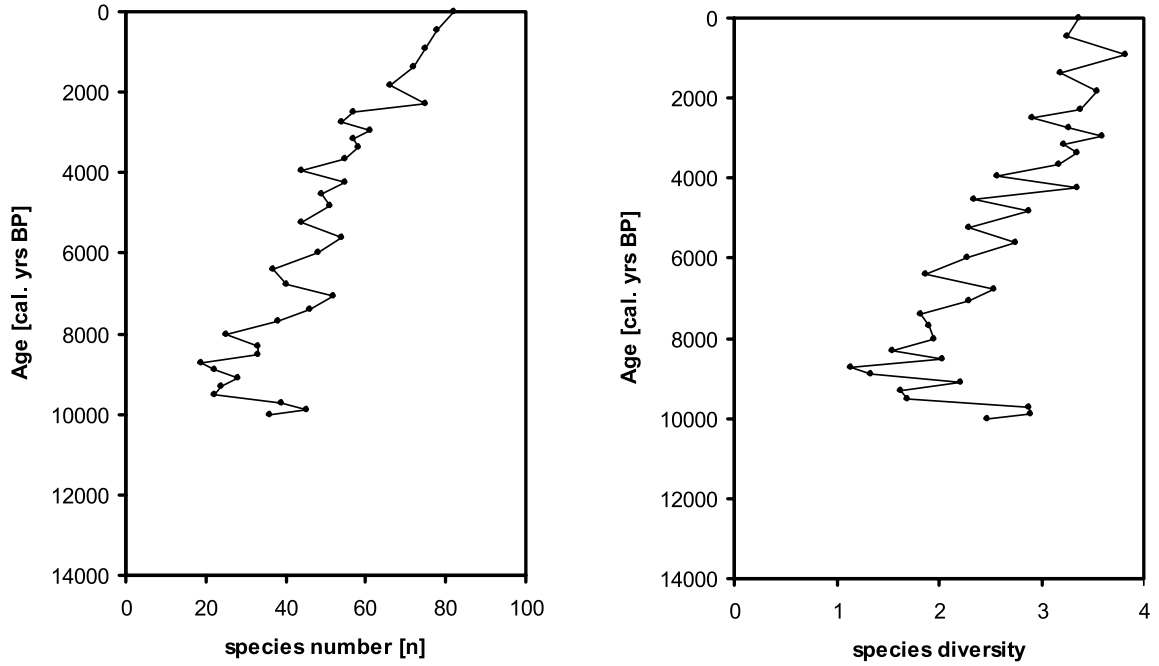


Figure V.21: Percent abundance of abundant diatom taxa at Lake Lilla Torkelsjön. The sums include taxa not shown in detail. JO: Lake Julma Ölkky, species sensu Lange-Bertalot and Metzelin (1996).



a. diatom species numbers b. diatom species diversity

Figure V.22: Species numbers and Shannon-Weaver species diversity index of diatoms at Lake Lilla Torkelsjön

garrensis, *B. neoexilis*, *B. styriaca*, *Frustulia crassinerva*, *F. saxonica*, and various *Naviculadicta* species. These occurred in low percentages but remained stable throughout the zone.

LTOdia-3: 135–65 cm depth; 4391–2619 cal. yrs BP

This zone was distinctly marked by the absence of *C. stelligeroides*, which was abundant in previous zones. In this zone, *Brachysira brebissonii* and *Fragilaria gracilis* attained the highest proportions at 20 and 30 %, respectively. Several other taxa, including *Brachysira*, *Frustulia*, *Navicula*, and *Naviculadicta* species, occurred with percentages between 5 and 10 %.

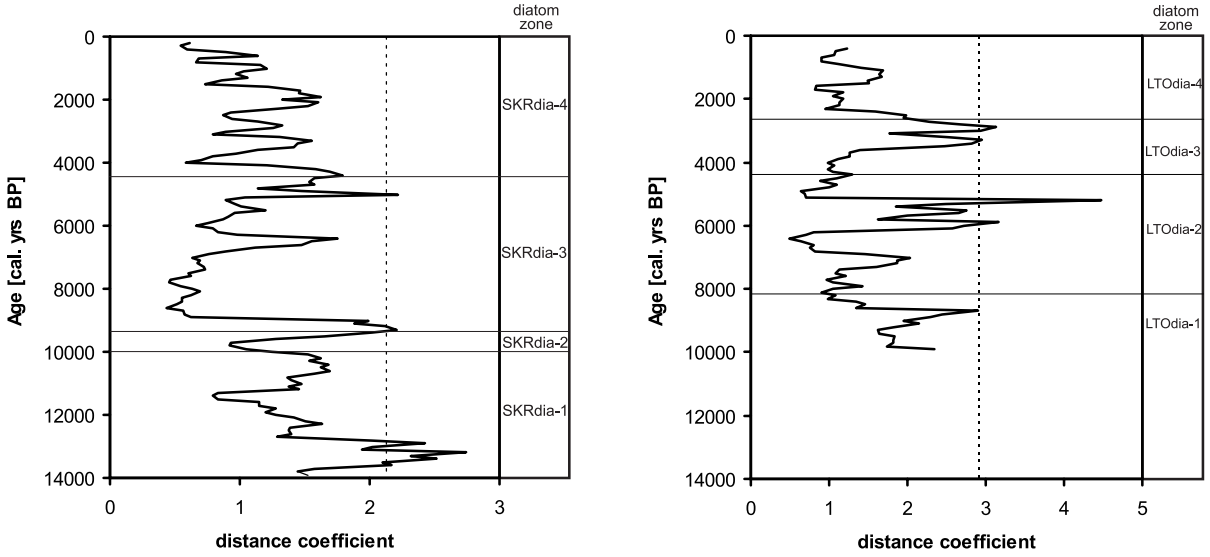
LTOdia-4: 65-0 cm depth; 2619–0 cal. yrs BP

This zone was characterised with a peak of 30 % of *Aulacoseira lacustris*, which had not occurred in the lake before. Several other *Aulacoseira*-species re-occurred that had not been present for at least 4000 years. *Fragilaria exigua* increased progressively until the top of the sediment core, from ca. 5 to > 25 %.

Ecological shifts and species richness

Benthic taxa were abundant at ca. 65 % in the lowermost sample. These decreased to a minimum of 20 % within the zone LTOdia-1 and then re-increased gradually throughout zone LTOdia-2 to around 50 %. Ca. 4250 cal. yrs BP (130 cm), planktonic taxa (e.g., *Cyclotella stelligera* and *C. stelligeroides*) abruptly declined. In this zone LTOdia-3, the assemblage was near-exclusively formed by benthic taxa. In zone LTOdia-4, planktonic taxa, including several *Aulacoseira* species and *Cyclotella cyclopuncta*, re-occurred (Figure V.21).

The number of diatom species at Lilla Torkelsjön began at ca. 40 species. Richness



a. rates of change SKR b. rates of change LTO

Figure V.23: Rates of diatom community change (chord distance per 100 yr) in Lakes a) Stora Kroksjön (SKR) and b) Lilla Torkelsjön (LTO). Vertical dotted line represents 95 % confidence limits based on Monte Carlo permutation tests with 5000 iterations.

decreased to a mean of 26 during the Boreal, between 10,000 and 8000 cal. yrs BP. After 8000 cal. yrs BP, a continuous rise in species numbers was observed (Figure V.22a). In the topmost sample, 82 species were found. The species diversity showed a similar pattern (Figure V.22b) with a decreasing trend until ca. 8700 cal. yrs BP and then a continuous increasing trend until present day. The low species diversity at 8700 cal. yrs BP is calculated for the sample containing 75% *Cyclotella stelligeroides*.

4.3 Rates of diatom assemblage change

Rates of change in the diatom community at Lake Stora Kroksjön reached significantly high values ($p < 0.05$) during three times during the last 14,000 years. These were a longer phase in the Allerød (between 13,600 and 12,900 cal. yrs BP), around 9300 cal. yrs BP, and a again around 5000 cal. yrs BP (Figure V.23a).

At Lilla Torkelsjön, the diatom community showed significant changes between 5900 and 5200 cal. yrs BP and between 3300 and 2900 cal. yrs BP. A near-significant peak was recorded at 8700 cal. yrs BP (Figure V.23b).

Mantel tests performed on the chironomid and diatom data sets of both sites revealed positive relationships between the distance matrices of both biota at Lake Stora Kroksjön as well as at Lake Lilla Torkelsjön. An additional Pearson correlation test confirmed the significance of this correlation with an r value of $r = 0.632$ ($p < 0.01$) and $r = 0.637$ ($p < 0.01$), respectively.

5 Pollen analysis

5.1 Pollen stratigraphy of Lake Stora Kroksjön

At Lake Stora Kroksjön, pollen analysis was generally carried out every 10 centimeters, beginning at 345 cm depth, resulting in a

total of 38 samples analysed. Application of the age–depth–model resulted in differing sedimentation rates and different temporal resolutions of 160 to 538 years between intervals. Two extreme values of 970 and 1250 years between intervals occurred at 315 and 325 cm. In the two lowermost samples, 345 and 335 cm, 1 cm^3 dry sediment yielded pollen count sums of 36 and 19, respectively, and were thus excluded from further investigation. Until ca. 11,100 cal. yrs BP, pollen count sums remained low (max. 313), but thereafter, a mean of 725 pollen grains per sample were counted throughout the Holocene (Figure V.24, see also Figure V.5).

The pollen record of Lake Stora Kroksjön could be divided into 4 statistically significant zones. Significant splits lay between 265 and 255 cm (SKR4/SKR5), 172.5 and 162.5 cm (SKR7/SKR8) and 62.5 and 52.5 cm (SKR10/SKR11). However, the sequence was divided in 11 local pollen assemblage zones (LPAZ) (Figure V.24) that could be related, more or less obviously, to the periods of the classical Blytt-Sernander sequence (e.g., Samuelsson, 1910, Figure V.26). As the first four pollen zones lay below the first dated horizon at 240 cm sediment depth, their age could only be estimated using the age-depth-model with time estimates (Figure V.4). It was, however, possible to relate them to the regional pollen assemblage zones established by Björck & Möller (1987), which in return was related to the GRIP event scale (Walker et al., 1999) by Ising (2001). The sequence thus comprised an estimated time span of 14,000 years (Figure V.26).

Local pollen assemblage zones

SKR1: *Pinus–Betula*–Poaceae–*Salix*–*Artemisia*
325–302.5 cm depth; 14,035–11,500 cal. yrs BP
The zone was characterised by an overall low number of pollen grains with relatively low values of arboral pollen. *Pinus* dominated with values of about 50 %, *Betula* occurred at around 20 %. Poaceae were present at a maximum of 16 %. *Salix* and *Artemisia* were present, at about 10 and 5 %, respectively. *Chenopodiaceae* were present around 2 %. The boundary of the zone was marked by an increase of *Betula* and a decrease of *Pinus*. The zone, though only comprising three samples, spanned a huge time interval considering the age-depth-model (see Chapter V.2) and incorporated both the Allerød and Younger Dryas periods.

SKR2: *Betula–Pinus*–Poaceae–*Artemisia–Salix*
302.5–292.5 cm depth; 11,500–11,185 cal. yrs BP
There was a distinct decrease in *Pinus* from ca. 80 % to 30 %, and a small rise in *Betula*. Poaceae reached their highest values throughout the whole sequence with values of 22 %. Ericaceae were represented in a proportion of up to 2 %. *Salix* and *Artemisia* were still present but decreased towards the end of the zone.

SKR3: *Betula–Pinus*–Poaceae
292.5–277.5 cm depth; 11,185–10,713 cal. yrs BP
Betula increased from around 30 to 61 % at the top of the zone. *Pinus* ranged from ca. 50 to 30 %. Poaceae decreased markedly, from about 20 to 5 %. *Juniperus* was present at around 2 %, but nearly disappeared at the end of the zone.

SKR4: *Pinus–Betula–Corylus*
277.5–260 cm depth; 10,713–10,162 cal. yrs BP
Betula decreased from around 60 % to 30 %, while *Pinus* became the dominant component at 62 %. *Corylus* and *Ulmus* were present in low abundances. *Artemisia* was present at 1.6 % at the bottom of this zone,

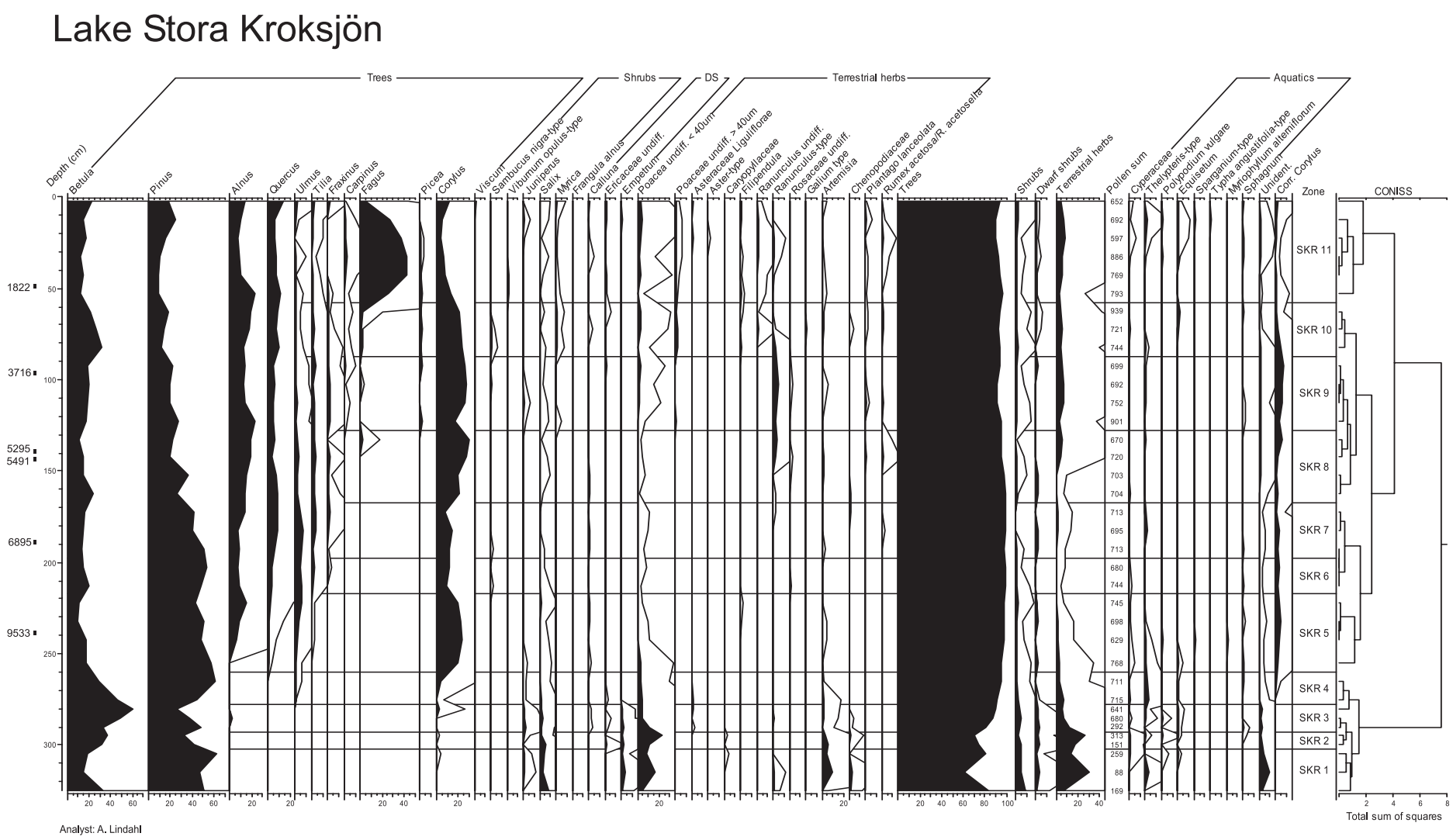


Figure V.24: The pollen percentage stratigraphy of Lake Stora Kroksjön. Hollow curve is 10 x exaggeration.

but disappeared at its top. Poaceae showed an unchanging presence of between 3 and 5 %.

SKR5: *Pinus–Corylus–Betula–Ulmus*
260–217.5 cm depth; 10,162–8346 cal. yrs BP
Invasion of *Alnus* and *Quercus* marked the beginning of the next zone. Zone SKR5 was dominated by *Pinus* between 43 and 57 %. There was an increase of *Corylus* from values of 4 to more than 20 %. *Alnus* increased continually to a value of 15 % by the end of the zone. *Ulmus* increased from 3 to 6 %. *Betula* was continuously present with values of around 15 %. *Quercus* appeared with low abundances, around 2 %. *Salix* and Poaceae were still present but with low values of around 1 %, and *Tilia* occurred for the first time.

SKR6: *Pinus–Ulmus–Alnus*
217.5–197.5 cm depth; 8346–7291 cal. yrs BP
The transition to this zone was characterised by a decrease in *Alnus* and *Corylus* and an increase in *Fraxinus*. *Pinus* dominated the assemblage at 50 % abundance, and *Alnus* values were ca. 8 %. *Corylus* was between 8-12 %. *Quercus* and *Ulmus* maintained a frequency of around 5 %. *Fraxinus* appeared in low abundance and *Tilia* was ca. 3 %.

SKR7: *Pinus–Tilia–Quercus*
197.5–167.5 cm depth; 7291–6193 cal. yrs BP
The transition to this zone was marked by an increase of *Quercus*. *Pinus* decreased to 40 % over this zone. *Alnus*, *Quercus*, *Ulmus*, and *Tilia* remained rather stable, at 10, 8, 6 and 3 %, respectively. *Corylus* was present around 11 % and *Fraxinus* about 2 %

SKR8: *Corylus–Pinus–Tilia–Alnus–Betula–Quercus*
167.5–127.5 cm depth; 6193–4831 cal. yrs BP
Corylus increased from 20 to 30 %, and *Alnus* was present between 15 and 20 %. *Tilia* and *Quercus* showed no changes in their abundance, around 5 to 10 %, respectively. *Pinus* and *Betula* are present at ca. 20 to 30 %. *Ulmus* was present around 1 %. *Fagus*-pollen were present for the first time. *Ranunculus* became comparatively abundant within the zone at 4 %.

SKR9: *Corylus–Pinus–Betula*
127.5–87.5 cm depth; 4831–3317 cal. yrs BP
Corylus was present at values between 20 and 25 %. There was a gradual decline in *Alnus*, from 15 to around 10 %, and in *Pinus*, from 30 to 20 %. *Betula* remained constant over the zone at 19 %. *Carpinus* and *Picea* were present for the first time. *Fraxinus* reached its maximum value with 2 %. *Ranunculus*-type pollen were present up to 5 % and Poaceae were present at 4 %.

SKR10: *Betula–Corylus–Alnus*
87.5–57.5 cm depth; 3317–2121 cal. yrs BP
This zone was characterised by a decline in *Betula*, from 30 to 15 %. *Corylus* remained constant at values of 20 %, similar to *Alnus*. *Ranunculus* decreased in this zone from 5 to < 1 %, and Poaceae were present at 3 %.

SKR11: *Fagus*
57.5–0 cm depth; 2121–0 cal. yrs BP
Fagus characterised this zone at > 40 % of the assemblage. *Betula*, *Pinus* and *Alnus* are present at 20, 20, and 15 %, respectively. *Corylus* ranged from 15 to 5 %. *Quercus* remained rather constant throughout the zone, reaching its maximum in the topmost sample. Poaceae became comparatively abundant, up to 5 %.

PCA analysis

PCA axis 1 sample scores of the pollen assemblages of Lake Stora Kroksjön

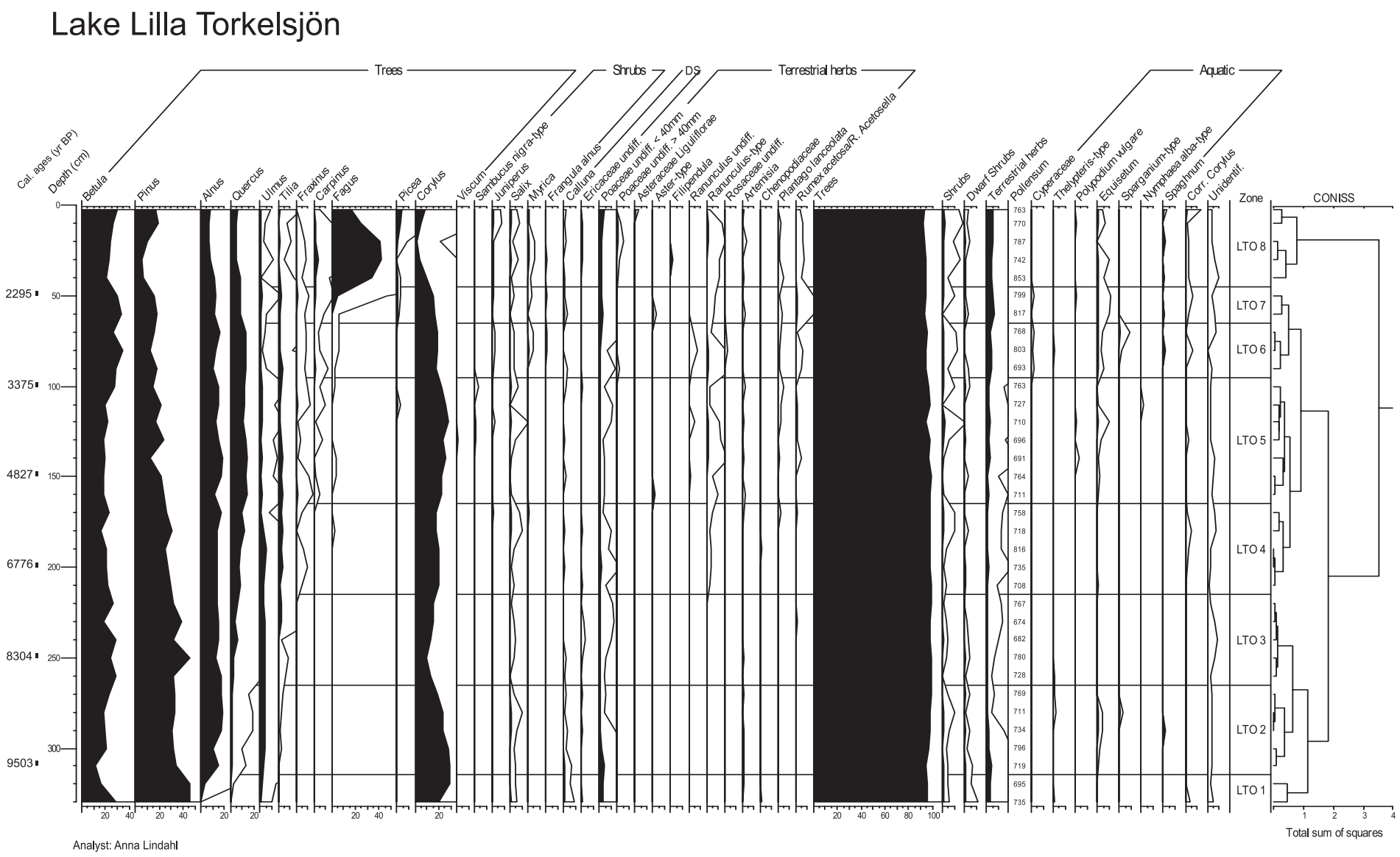


Figure V.25: The pollen percentage stratigraphy of Lilla Torkelsjön. Hollow curve is 10 x exaggeration.

(λ_1 = 0.463) began > 1 and remained so from 14,000 to nearly 10,000 cal. yrs BP (Figure V.17a). Values dropped to ca. -0.5 by 9000 cal. yrs BP, and continued a long decreasing trend to < -1 by 2000 cal. yrs BP. After this time, values increased slightly to -0.4 at the core top.

5.2 Pollen stratigraphy of Lake Lilla Torkelsjön

At Lake Lilla Torkelsjön, pollen samples were counted every 10 centimeters, beginning at 330 cm depth. A total of 34 samples were analysed, yielding a temporal resolution of 200 to 400 years between samples. In all samples, a total of 680 to 800 pollen grains were counted.

The sequence of Lilla Torkelsjön spanned approximately 10,000 ^{14}C years. The bottom samples with an increase of *Corylus* and a decrease of *Betula* and *Pinus* point towards the Preboreal/Boreal transition (Berglund, 1966a), as does a linear extrapolation from the lowest ^{14}C date by age/depth conversion. Two statistically significant splits were detected, dividing the sequence between 220 and 210 cm (LTO3/LTO4) and 50 and 40 cm (LTO7/LTO8). However, eight local pollen assemblages zones (LPAZ) were distinguished by the pollen analyst (Figure V.25).

Local pollen assemblage zones

LTO1: *Pinus–Corylus–Betula*
332–315 cm depth; 9950–9603 cal. yrs BP
The zone was characterised by high proportions of *Pinus*, *Corylus* and *Betula* at 45, 25 and 20 %, respectively. *Alnus* and *Quercus* pollen increased to ca. 8 and 1 %, respectively, by the end of the zone. Poaceae were present at 3 %. Other shrub and dwarf shrub pollen such as *Salix* and *Calluna* were present in low abundance.

LTO2: *Pinus–Corylus–Betula–Alnus*
315–265 cm depth; 9603–8604 cal. yrs BP
This zone was characterised by *Alnus* reaching 18 %, while *Pinus* declined relative to the preceding zone, to 30 %. *Corylus* decreased from around 25 to 19 % by the end of the zone. *Betula* ranged between 20 and 30 %. *Ulmus* and *Quercus* remained at constant percentages of 1.5 and 4 %, respectively. *Tilia* appeared in very low values. The abundance of small Poaceae-pollen decreased towards the upper part of the zone.

LTO3: *Pinus–Betula–Alnus*
265–215 cm depth; 8604–7234 cal. yrs BP
Pinus and *Betula* were present at around 35 and 25 %, respectively. *Corylus* ranged between values of 9 and 15 %. *Quercus* occurred at 5 % and *Tilia* increased to about 4 %.

LTO4: *Pinus–Betula–Corylus–Alnus*
215–165 cm depth; 7234–5412 cal. yrs BP
The zone was dominated by *Pinus, Betula*, and *Corylus* at 30, 20 and 20 %, respectively. *Alnus* and *Quercus* were present at 14 and 8 %, respectively. *Fraxinus* and *Fagus* were found for the first time. *Ulmus* showed a marked decline near the zone end. Among the terrestrial herbs, *Ranunculus*-type pollen was found for the first time.

LTO5: *Corylus–Betula–Pinus–Alnus*
165–95 cm depth; 5412–3267 cal. yrs BP
Corylus, Betula, Pinus had similar abundance at ca. 20 %. *Fraxinus* became slightly more abundant than in the previous zone. *Carpinus* appeared for the first time and remained at low percentages. *Fagus* and *Picea* occurred, but in low abundance. *Plantago lanceolata* -pollen were found continuously in low values from the upper half of this zone onwards.

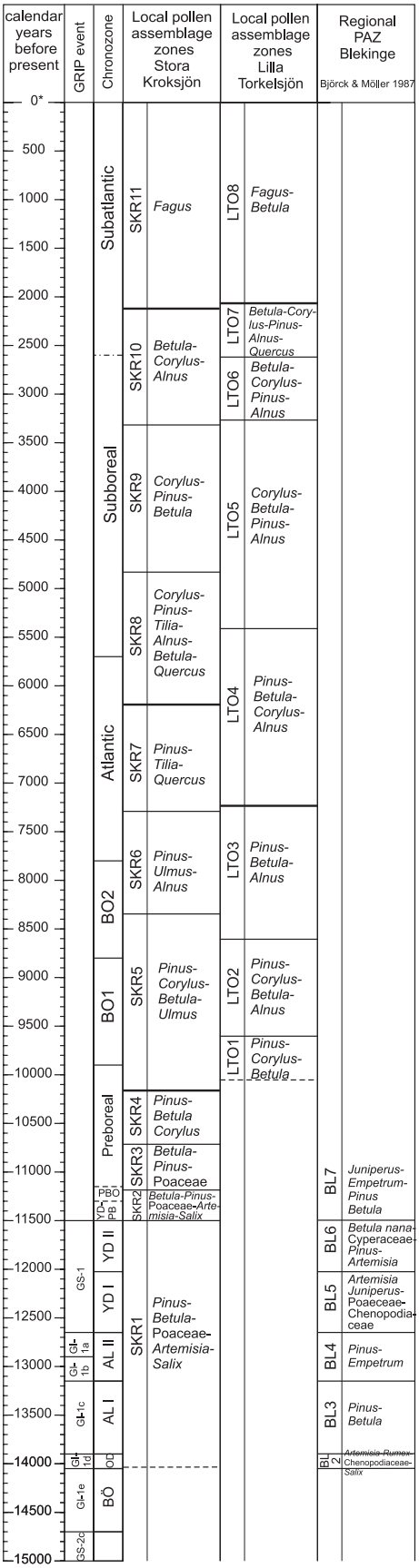
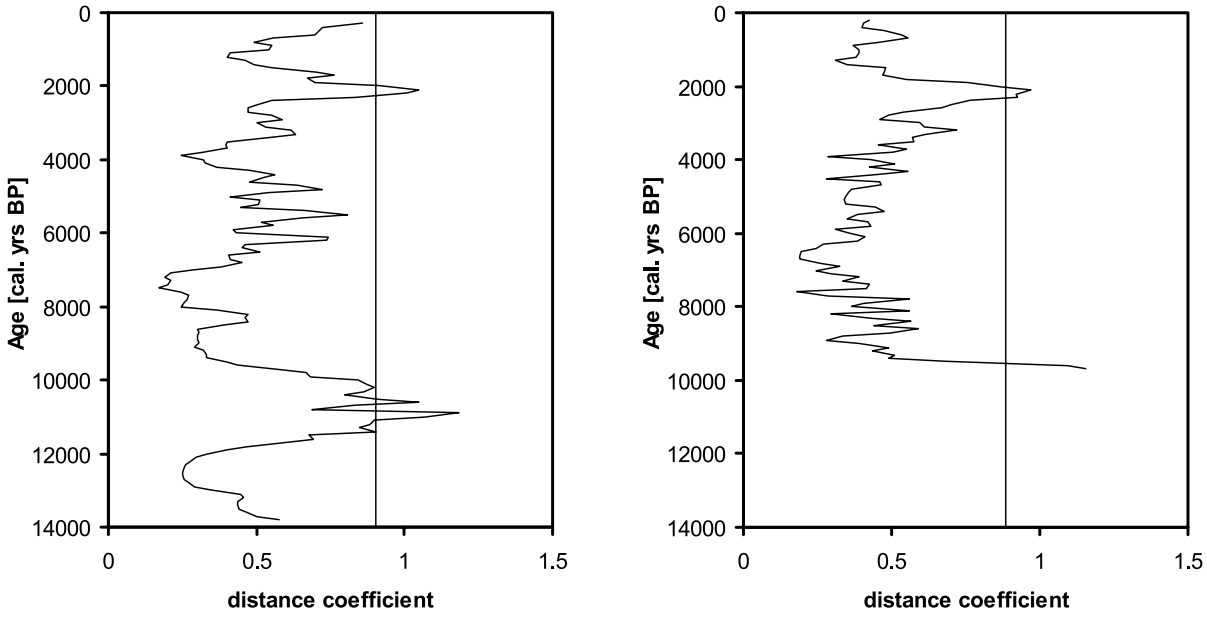


Figure V.26: Correspondence of local pollen assemblage zones (LPAZ) from the studied sites to the regional pollen assemblage zones from Färskesjön (Björck and Möller, 1987) and the pollen zones for southern Sweden after Mangerud et al. (1974). Fat lines mark significant zone boundaries assessed by sum-of-squares optimal partitioning criteria tested on a broken-stick model. Dash-dotted lines mark the lower boundary of pollen analysis. Abbreviations: AL = Allerød, YD = Younger Dryas, PB = Preboreal, PBO = Preboreal Oscillation, GS, GI = Greenland Ice core record stadial and interstadial events. 0*: reference year 1950 A.D. (Stuiver et al., 1998). Dash-dotted line at the SB-SA boundary: Boundary still in discussion.



a. rates of change SKR b. rates of change LTO

Figure V.27: Rates of vegetation change (chord distance per 100 yr) in a) Stora Kroksjön (SKR) and b) Lilla Torkelsjön (LTO). Vertical dotted line represents 95% confidence limits based on Monte Carlo permutation tests with 5000 iterations.

LTO6: *Betula–Corylus–Pinus–Alnus*
95–65 cm depth; 3267–2619 cal. yrs BP
Betula became markedly more abundant in this zone than earlier in the core, reaching 35 %. *Pinus, Alnus*, and *Quercus* remained stable at 16, 13 and 10 %, respectively. *Corylus* occurs at 20 % abundance. *Ulmus* disappears nearly completely from the sequence. *Fagus* and *Carpinus* were found continuously, but their percentage remained low. There were distinct increases in Poaceae, *Rumex*- and *Ranunculus*-type pollen.

LTO7: *Betula–Corylus–Pinus–Alnus–Quercus*
65–45 cm depth; 2619–2066 cal. yrs BP
Betula was the most abundant pollen type at 30 % of the assemblage. *Pinus* and *Corylus* were both present at 15 %, and *Alnus* and *Quercus* occurred at 12 and 10 %, respectively. *Fagus* increased to about 5 % by the end of this zone, and *Picea* occurred at nearly 1 %.

LTO8: *Fagus–Betula*
45–0 cm depth; 2066–0 cal. yrs BP
This zone was characterised by an increase of *Fagus* to ca. 40 %, however, it declined to about 17 % by the zone end. *Corylus* ranged between 10 and 2 %, and *Pinus* had a mid-zone minimum of 5 %. *Quercus* decreased relative to the preceding zone, to 5 %. *Alnus* occurred around 8 %. *Picea* pollen became most abundant in the topmost samples.

PCA analysis

PCA axis 1 sample scores ($\lambda_1 = 0.554$) of the pollen assemblages showed values beginning around -1, and increasing to zero by ca. 4800 cal. yrs BP (Figure V.17b). Sample scores fell slightly to -0.4 by 3800 cal. yrs BP, and thereafter increase to > 2 by 2000 cal. yrs BP. Values decline slightly thereafter, but remain > 1 by the top of the core.

5.3 Comparison of the pollen assemblage zones at Stora Kroksjön and Lilla Torkelsjön

The correspondence of pollen zones and boundaries at Stora Kroksjön and Lilla Torkelsjön differed somewhat throughout the Holocene (Figure V.26). The lower boundary of the Boreal was asynchronous lying at ca. 10,000 and 9700 cal. yrs BP. The upper boundary of BO2 occurred at 8600 and 8400 cal. yrs BP, respectively, suggesting vegetation had reached equilibrium in Blekinge. The Atlanticum/Subboreal transition was not clearly identified with any particular pollen zone boundary at Lake Stora Kroksjön or LTO. However, important regional thresholds appeared to have been crossed at 7300 cal. yrs BP, 3400 cal. yrs BP, and 2100 cal. yrs BP. These correspond approximately to the BO2/Atlanticum and the Subboreal/Subatlanticum boundaries.

Rates of change in the pollen record at Lake Stora Kroksjön reached significantly high values ($p < 0.05$) twice during the last 14000 years. Significant species turnover rates were attained during the Preboreal (between 11,400 until 10,200 cal. yrs BP) and around 2100 cal. yrs BP, when the expansion of *Fagus* gained momentum (Figure V.27a). Very similar rates of changes within the pollen record are found at Lake Lilla Torkelsjön. Significant vegetational change was registered at the end of the Preboreal and 2100 cal. yrs BP, when beech forest became dominant (Figure V.27b).

Chapter VI

Discussion

1 History of Lake Stora Kroksjön

1.1 Loss on ignition and core parallelisation

Loss on ignition (LOI) is used as a proxy for the organic and inorganic carbon content of sediment samples. It gives information about productivity in the lake and its catchment. The results of combustion can differ considerably (Heiri et al., 2001), depending on sediment composition, sample size, length of combustion time or combustion temperatures. In this study, exposure time of 4 hours and a comparable sample size (0.31 g dry weight, SD 0.04) ensured best conditions for low errors (Heiri et al., 2001), which was important as core parallelisation was done using LOI curves. A combustion at 950 °C was not performed, as the inorganic carbonate content of the sediments analysed was expected to be negligible. Alkalinity monitored by Blekinge Länstyrelsens Miljöövervakning (Blekinge County Administrator Environment Monitoring Agency) recorded a mean of 0.35 meq L^{-1} between 1990 and 1998 at Stora Kroksjön. Both lakes have been limed twice (1986 and 1990) in order to counteract airborne acidification (S. Björk, pers. comm.).

LOI as a measure of the amount of organic carbon within the sediment incorporates different signals from the system and its surroundings. Variations in LOI can reflect:

- changes in the productivity of the lake and thus in organic deposition (autochthonous carbon)
- differing influx of terrestrial organic material from the catchment (allochthonous carbon)
- variation in the input of clastic material from the catchment due to differing erosion processes (sediment yield)
- variation in the sedimentation of biogenic silica (from e.g., diatoms)

These factors have to be borne in mind, when interpreting changes in LOI. Nevertheless, such changes are informative, as they are 'real' and absolute measured values, whereas variation in species curves may be artificial due to the interdependence of percentages.

Correct parallelisation of sediment cores is fundamental for the correct interpretation of sequences comprising several overlapping cores. There is always the risk that sequences have not been correctly matched. Poor parallelisation may be seen as a doubling of signals at the boundary of two core parts, whereas the absence of a segment is difficult to detect.

In this study, core parallelisation was performed by depth-from-water-sediment-interface, visual inspection of stratigraphic markers, and matching of the LOI curves.

This worked extremely well for the overlapping sequences at Lake Stora Kroksjön, as only the middle part of SKR1 2-4m shows a slightly higher aberration from the near-identical LOI curve of SKR1 1-3 and SKR1 1.5-3.5 (Figure V.2a). Errors within the age-depth-model due to incorrect parallelisation are expected to be small because of the similar absolute values and patterns of the LOI curves. The part of core SKR1 2-4m between 270 and 240 cm absolute depth, which showed greater aberrations in LOI values, may have experienced some compression, but is inconsequential as no samples from this core part entered into the analysis.

1.2 Sediments, core chronology and dating

In both lakes, soft, uniformly black-brown algal gyttja without macroscopic lamina were deposited during the Holocene. This points toward stable environmental conditions both within the lakes and the lake catchments, even though there is a gradual increase in organic deposition observed at Lake Stora Kroksjön contrasting with high organic deposition at Lake Lilla Torkelsjön from the base of the sequence (see Chapter VI.2.2). The materials at the base of the cores differ considerably and reflect the different environmental situations under which the two sites became independent lake basins. Blekinge's coast started to become deglaciated during the Bölling chronozone, around 14,600 cal. yrs BP (Lundqvist and Wohlfarth, 2001), which correlates with the -100 varve year of Ringberg's (1979) varve chronology. The site of Lake Stora Kroksjön lies between the -20 and 0 equicess (geographical lines of equal deglaciation time) and had thus become ice-free 80 to 100 years later than the current coastal region. Below the highest coast line, ice recession happened transgressively, which means that the emerging areas became directly inundated by the waters of the Baltic Ice Lake which formed from the glacier meltwaters (Björck and Möller, 1987). The basin of Lake Stora Kroksjön, lying below the highest coastline, was thus part of the BIL from the time of its emergence under the ice sheet.

The basal clay sediments of Lake Stora Kroksjön reflect the highly dynamic sedimentary environment of the BIL, where varved and unvarved clays were deposited at high rates of accumulation (Björck and Möller, 1987). As the age of the basal clay was not determinable for lack of marker horizons and terrestrial macrofossils, the age-depth-relation was modelled using the sedimentation rates of the relevant time period from the 'Farslycke' site (Ising, 1998). This approach may appear somewhat improvised, but is more appropriate than extrapolating sedimentation rates from those calculated from above the isolation level at 322.5 cm. These rates were dramatically lower and would have resulted in ages much older than the actual deglaciation of the locality. Moreover, the BIL clays did not yield sufficient biological remains material to be included in the diatom or chironomid analysis and is thus not suitable for paleoenvironmental reconstructions.

As there was no dated material from Lake Stora Kroksjön below 240 cm (ca. 9530 cal. yrs BP), the estimated dates of two important stratigraphic events were used to establish the age-depth model below 240 cm - firstly, the time of isolation of the lake basin from the BIL and secondly, the Late Weichselian/Holocene boundary. The shoreline displacement curve of the BIL in Blekinge is well established by Berglund (1966a) and Björck (1979). Björck (personal communication) pinpoints the timing of isolation of a site at 51 m a.s.l. at ca. 14,000 cal. yrs BP. The isolation of the Lake Stora Kroksjön basin is marked in the core by the

change in lithological composition, namely the beginning of organic sedimentation with the organic carbon content rising from 0.5 to about 5 % at 322.5 cm. The second distinct change marks the YD/PB transition at 297.5 cm, when organic carbon starts to be deposited in increasingly greater amounts, eventually reaching 40 % during the Atlanticum chronozone. Sedimentation rates drop to extremely low values of ca. 0.08 mm yr^{-1} subsequent to isolation, which is also reported from Farslycke, where sedimentation rates remained low during the begin of the Holocene (Ising, 1998) . At Lake Stora Kroksjön, sedimentation rates rise to values around 0.25 mm yr^{-1} after the end of the Younger Dryas and remain stable for the rest of the sequence.

The pattern of LOI at Lake Stora Kroksjön is in close connection to the isolation of the lake basin from the Baltic Ice Lake. The grey clay deposits of the BIL are replaced by grey-greenish gyttja clay, deposited in the newly isolated lake. Sediments gradually become more enriched with organic material, as autochthonous productivity is initiated. High algal productivity in freshly isolated basins and an initial rise in LOI may have been favoured by several factors. Firstly, little competition exists from other plant communities that favours the expansion. The habitats were virgin in late-glacial lakes especially in recently isolated lakes. Secondly, a good supply of nutrients was available. Additionally, the rising temperatures favour the organic production, as rates of metabolism are controlled by temperature. Lastly, the improvement of the light climate in a lake, e.g., a development from a clayey water to a transparent water column allowed increased productivity (Berglund, 1966a). The prolongation of the ice-free period during the year played an additional role in causing an increase in LOI. Still, it is not until the favorable conditions of the Holocene that lake productivity really started to increase. The development of a closed terrestrial vegetation canopy (LPAZ SKR3, approximately 11,200–10,700 cal. yrs BP) may also have resulted in decreased soil erosion in the catchment, thus further increasing the relative proportion of organic components in the sediment. LOI eventually reached 40 to 45 % at ca. 120 cm (4550 cal. yrs BP) and remains so until present day.

1.3 The chironomid record

The late-glacial

Older Dryas and Allerød; 14,000–12,600 cal. yrs BP

In the grey Baltic Ice Lake clays below 322.5 cm, only low concentrations of chironomid head capsules were found, indicating that this aquatic environment held unsuitable conditions for colonisation by a diverse midge fauna. Low food availability due to low productivity may be a relevant factor, as well as physical factors like wave action and a high debris load of the BIL waters. However, Lake Stora Kroksjön shows a diverse midge assemblage directly after the isolation from the BIL, in chironomid zone SKR1-1. In the first sample yielding enough head capsules for further analysis (322.5 cm, 14,000 cal. yrs BP), already 10 taxa are registered (Figure VI.1). Among the earliest colonisers found as fossils in Lake Stora Kroksjön were *Monodiamesa*, *Protanypus*, *Micropsectra*, *Procladius*, *Heterotrissocladius grimshawi*, *Microtendipes*, and *Chironomus anthracinus*. These taxa point towards a cool, oligotrophic and oxygen rich environment, considering their preferred present day habitats. *Microtendipes*, dwelling in coarse littoral substratum (Brodersen and Lindegaard, 1999), is the only true littoral species present in high abundance, though Hofmann (1971a) also reports a habi-

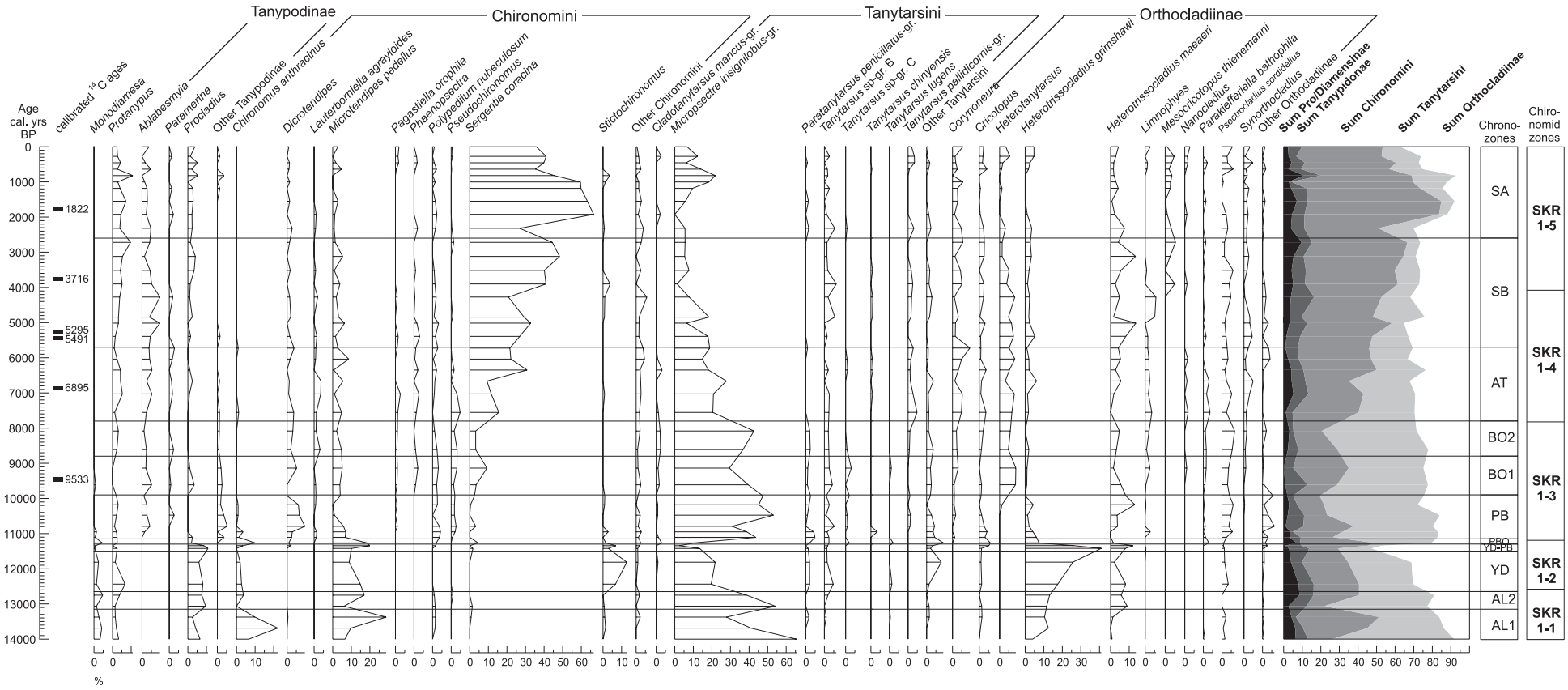


Figure VI.1: Percent abundance diagram of the chironomids of Lake Stora Kroksjön with respect to the late-glacial and Holocene chronozones. Abbreviations: AL = Allerød, YD = Younger Dryas, PB = Preboreal, PBO = Preboreal Oscillation, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum

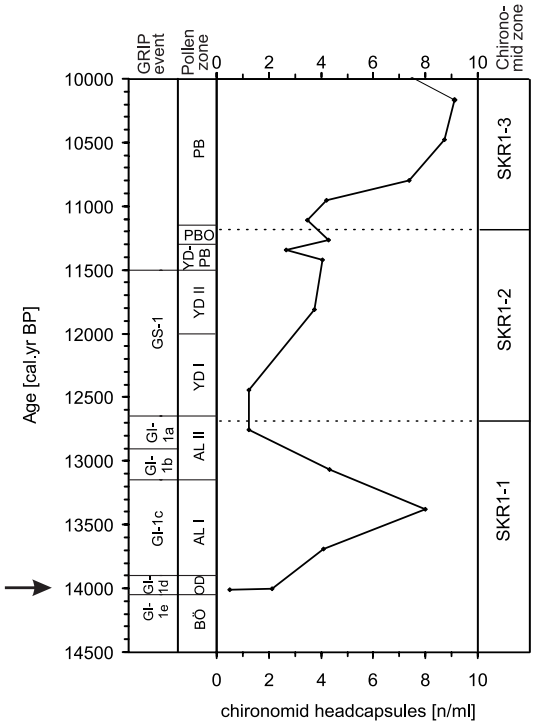


Figure VI.2: Chironomid head capsules concentration in the late-glacial sediments of Lake Stora Kroksjön. Abbreviations: Bö = Bölling, OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PB = Preboreal, PBO = Preboreal Oscillation, GS, GI = Greenland Ice core record stadial and interstadial events. The arrow marks the point of isolation from Baltic Ice Lake.

tat preference change for *Micropsectra* from the littoral zone during Younger Dryas to profundal habitats from the Preboreal onward. The first sediment levels of the isolated Lake Stora Kroksjön reveal the typical midge fauna of a cool, oligotrophic environment similar to other late-glacial midge assemblages in central and northern Europe (Heiri et al., 2003b; Brooks and Birks, 2000a; Brooks, 2000; Alm and Willassen, 1993).

Recently deglaciated lakes may experience an increase in nutrient level during the first one or two centuries after deglaciation (Berglund, 1966a; Engstrom et al., 2000). Conditions were thus favorable for high algal productivity, providing an abundant food resource for the chironomids and allowing for a fast increase in chironomid density, documented by the strong increase in head capsule concentration during the early Allerød (Figure VI.2). Low intra- and interspecific competition and a presumably low initial predation pressure by fish, as well as the temperate climate conditions of the Allerød will have further favoured a rapid increase in chironomid density and diversity. Such a high initial nutrient level may favour the immigration of a chironomid community typical for meso- to eutrophic conditions with high temperature optima (Brodersen and Anderson, 2002), among which *Chironomus* can be quite abundant. A study examining the initial chironomid population of lakes freshly isolated from the Northsea (Solem et al., 1997) during the early Holocene also report *Chironomus* as one of the first colonisers, although the studied lakes otherwise developed a species assemblage typical for low-trophic conditions. Hence, the initial chi-

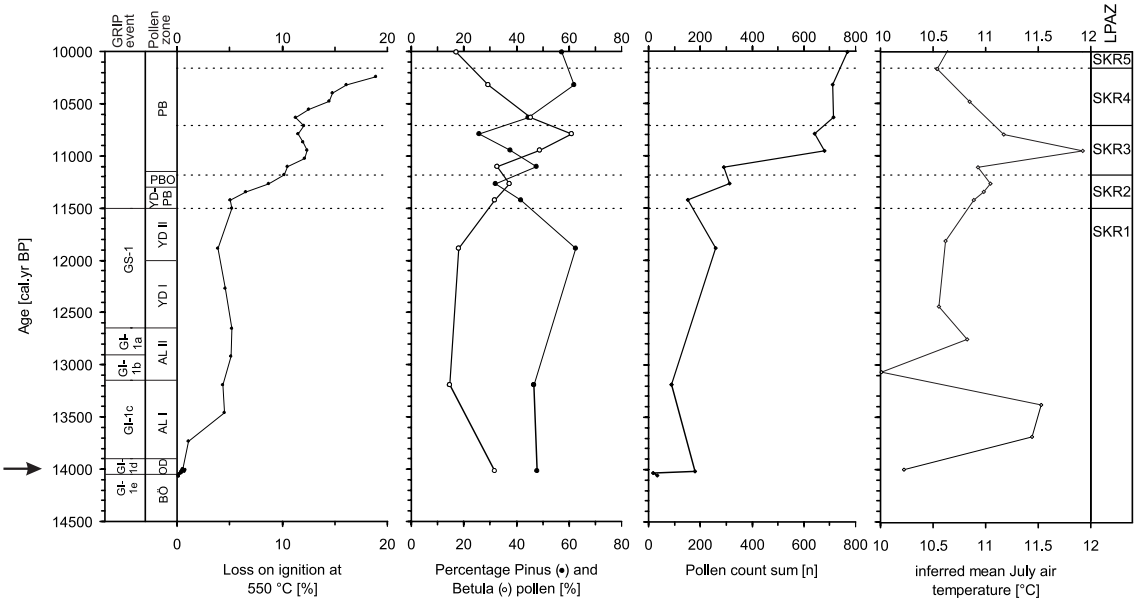


Figure VI.3: Loss on ignition, tree and herb pollen percentages, total pollen sums and inferred mean July air temperatures at Lake Stora Kroksjön. Abbreviations: Bö = Bölling, OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PB = Preboreal, PBO = Preboreal Oscillation, GS, GI = Greenland Ice core record stadial and interstadial events. The arrow marks the point of isolation from the Baltic Ice Lake. LPAZ = local pollen assemblage zone

ronomid assemblage of Lake Stora Kroksjön may possibly have been for a short period (the first sample) nutrient-controlled rather than temperature-controlled.

The chironomid-inferred mean July air temperature reconstruction of this period points towards a distinct warming at the onset of the Allerød warm interstadial, as inferred temperatures increased to ca. 11.5 °C (Figure VI.3). On the boundary of the Early to Late Allerød, the Gerzensee Oscillation (GRIP event GI-1b, Schwander et al., 2000) is captured by the reduction of the more temperate taxa *Chironomus anthracinus* and *Microtendipes*, even though species more cold-adapted than *Micropsectra insignilobus* gr. (e.g., *Monodiamesa* and *Heterotrissocladius maeaeri*) do not increase strongly. The Gerzensee Oscillation (also termed Killarney Oscillation in North America, Levesque et al., 1993) was a minor cooling oscillation with a magnitude of probably less than 1 °C in the Swiss Alps (Lotter et al., 2000), and thus well within the model error. Nevertheless, the reconstruction infers the lowest temperatures (10.0 °C) registered throughout the whole sequence of Lake Stora Kroksjön, likely caused by the dominance of *M. insignilobus* gr..

Younger Dryas; 12,600–11,500 cal. yrs BP

The Younger Dryas period is framed by the highest rates of change of the chironomid species composition (Figure V.12) recorded at Lake Stora Kroksjön, with a notable peak marking the beginning of the cool period and another one marking its end. The two samples representing the Younger Dryas event also record a decrease in chironomid density (Figure V.8, zone SKR1-2). The cold-adapted taxa *Heterotrissocladius grimshawi* and *Stictochironomus* increase, whereas other taxa like *Micropsectra insignilobus* gr. and *Chironomus* decrease or even disappear

(e.g., *Sergentia* and *Polypedilum*). The minor positive response from *Procladius* supports this concept. No thermal response is observed with taxa normally associated to cold conditions, such as e.g., *Monodiamesa* and *Tanytarsus lugens* type.

The thermal response of the midge fauna to the Younger Dryas event seems less pronounced here than in other late-glacial sequences (e.g., Brooks and Birks (2000a), where temperate taxa such as *Cricotopus*, *Psectrocladius sordidellus* gr. or *Microtendipes* disappear completely from the fauna), suggesting that the magnitude of cooling might have been smaller in Blekinge than in northwestern Europe. This idea has, however, not been confirmed at other sites in southern Sweden or similar latitudes. The chironomid-inferred temperature for the Younger Dryas is about 10.5 °C, whereas it has been estimated to have been between 7.5 and 9 °C at Whitrig Bog, Scotland (Brooks and Birks, 2000b), and 9.5 to 10 °C at Kråkenes Lake, western Norway (Brooks and Birks, 2000a), two sites at comparable altitudes (125 and 38 m a.s.l., respectively). At both of these sites, the magnitude of the temperature decline was about 2 °C. It should be expected that a site, lying in a comparatively more continental climate area as Blekinge does, might be influenced more strongly by a climate deterioration, since the regional climate is not buffered as efficiently by the Gulf stream. At Lake Stora Kroksjön, inferred Younger-Dryas temperatures are slightly warmer than in western Scandinavia or Scotland and the temperature decline is less than 1 °C. As all three sites have been reconstructed with the same transfer function data set, analogue problems and model edge effects may play a role in the discrepancy of inferred temperatures at the sites not originating from the area covered by the calibration set. Lake Stora Kroksjön is deeper than Kråkenes Lake (2.4 m) and the late-glacial Whitrig Bog (5-8 m). The larger water volume may have led to increased buffering of the sublittoral and profundal communities and thus protected species with higher temperature optima and wide tolerances (e.g., *Chironomus anthracinus* type and *Microtendipes pedellus*) from going extinct.

It is noteworthy to observe that *Micropsectra insignilobus* gr. declines during the Younger Dryas, even though this taxon showed a lower thermal optimum in the Norwegian calibration set than either *Heterotrissocladius grimshawi* or *Stictochironomus*. Other ecological factors must have had an overriding influence on the competitiveness of *M. insignilobus* gr. with respect to other species. These could be substrate composition or food availability in the lake profundal. Brooks (2000) demonstrated the importance of local environmental conditions at four different sites in the Swiss Alps, where the chironomid species assemblages react quite differently to climate oscillations, but nevertheless the large-scale climatic trends are always detectable. The fact that *M. insignilobus* gr. regains high abundances and remains the dominant taxon, even during the Holocene climate maximum, further supports the assumption that additional factors other than climate govern the distribution of this taxon. As the *Micropsectra insignilobus* gr. probably incorporates several species, the distinction of which is not possible on subfossil material, it is possible that at Lake Stora Kroksjön, a different species with a higher thermal optimum might be involved than those present in the Norwegian calibration set.

The Postglacial

The postglacial development of the chironomid fauna can be divided into three phases, roughly corresponding to the Preboreal and

Boreal, where *Micropsectra* dominates the assemblage (chironomid zone SKR1-3), 7820 to 4100 cal. yrs BP (Atlanticum and early Subboreal) when *Sergentia* and *Micropsectra* are more or less equally abundant, though the first is increasing whereas the latter is decreasing slowly (chironomid zone SKR1-4), and 4100 cal. yrs BP to the present, when *Sergentia* is the dominant taxon (chironomid zone SKR1-5). Among the other chironomid taxa, conspicuous changes in abundance are not apparent after ca. 9900 cal. yrs BP, though some species immigrate or disappear. E.g., *Pseudochironomus*, and less conspicuously *Dicrotendipes*, *Pagastiella orophila* and *Cladotanytarsus mancus*, thrive predominantly during the earlier periods of the Holocene until ca. 7000 cal. yrs BP, when these warm-adapted taxa found suitable conditions.

Preboreal and Preboreal oscillation; 11,500–9900 cal. yrs BP

The climate warming at the end of the lateglacial period led to a development of woodland dominated initially by birch. This expansion was shortly interrupted by the Preboreal oscillation (PBO), a climate reversal initially described by the decreasing δ^{18}O values from the GRIP stable isotope record from Greenland (Björck et al., 1996) and confirmed by abundant paleoproxy evidence (e.g., Björck et al., 1997; Schwander et al., 2000). The PBO begins at around 11,300 and is considered to have lasted between 150 and 250 years. It was possibly triggered by a catastrophic meltwater discharge from the glacial Lake Agassiz (a meltwater lake south of the Laurentide Ice Sheet in North America) (Fisher et al., 2002), influencing ice-cover and thermohaline circulation in the North Atlantic, as proposed by Björck et al. (1996) and Hald and Hagen (1998). A plateau in the LOI, declining pollen count sums and the small decline of *Betula*-pollen are signals of the PBO in southern Sweden (Björck et al., 2002, 1997). These signals are captured by the 290 cm sample from Lake Stora Kroksjön, dated 11,107 cal. yrs BP by the age-depth model (Figure VI.3, lowest sample of pollen zone SKR3). However, the temperature signal is not clearly reflected in the midge fauna, likely because it is masked by the community reaction to the general warming trend, i.e., cool-adapted taxa such as *Heterotrissocladius grimshawi* and *H. maeaeri* decline distinctly at the onset of warm conditions, while *M. insignilobus* gr. has a brief minimum. Many other taxa undergo distinct, albeit small-scale variations e.g., *Chironomus anthracinus*, *Monodiamesa* and *Microtendipes* reach their maximum abundance. Due to the coarse temporal sample resolution of about 150 years, it is difficult to discern the effects of the postglacial warming from the short climate cooling during the PBO, which in itself only lasted for about 150-250 years. The temperature reconstruction infers slightly lower temperatures for sample 290 cm, even though the magnitude of the decline is low and well within the prediction error of the model (1.01 °C).

The Preboreal period (lowest part of chironomid zone SKR1-3) brought about a massive species immigration into Lake Stora Kroksjön. Species numbers and diversity increase, even though *M. insignilobus* gr. dominates the assemblage for several thousand years. A diverse, littoral chironomid fauna is now established, represented by taxa such as *Corynoneura scutellata*, *Limnophyes*, *Parakiefferiella bathophila*, *Ablabesmyia*, *Tanytarsus pallidicornis*-gr., *T. chinyensis*, *Dicrotendipes*, and *Lauterborniella agrayloides*. This species assemblage indicates the presence of a well developed macrophyte belt in the lake littoral. The chironomid density increases with productivity, indicated by the increasing trend in LOI. The predacious tanypod *Procladius* disappears for some time and two more tanypod genera, *Ablabesmyia* and *Paramerina*, become established. There

are three taxa that disappear completely during the Preboreal, only to reappear in very long intervals and in very low proportions; for the cold-stenothermic taxon *Monodiamesa*, the thermal conditions were obviously unfavourable, whereas it is difficult to pinpoint the ecological factors that might have led to exclusion of *Chironomus anthracinus* and *Stictochironomus* from the species assemblage. As *Stictochironomus* is reported to be cold-adapted (Brundin, 1949; Korhola et al., 2002), its response may be related to climate. *Chironomus anthracinus*, however, is normally found in environments of higher productivity, and is tolerant of low oxygen concentrations (Clerk et al., 2000). As the lake is still oligotrophic (LOI $\approx$ 23 %), *C. anthracinus*, though being a pioneer taxon at this lake, might not have been able to deal with increasing competition arising from an increasing chironomid density and diversity.

The change from the late-glacial to the post-glacial species assemblage is delineated by the multivariate analysis. In the PCA analysis (Figure V.7), sample scores of the zones SKR1-1 and SKR1-2 appear close together, representing late-glacial assemblages that contrast with the species communities of the Holocene zones SKR1-3–SKR1-5, and clearly depict the change in assemblage character. Because PCA uses Euclidean distance instead of chord distance as a dissimilarity index, this result disagrees slightly with the CONISS cluster analysis (dendrogram in Figure V.6) and the zonation by the broken stick model, which place the significant community change at 7800 cal. yrs BP (between SKR1-3 and SKR1-4) at the end of Boreal 2. It thus divides the chironomid community at Lake Stora Kroksjön between *Sergentia* and *Micropsectra* scarcity and abundance.

Boreal to Subatlanticum; 9900–0 cal. yrs BP

The most obvious chironomid signal in Lake Stora Kroksjön is the dominance shift from *Micropsectra* to *Sergentia coracina*, both inhabitants of profundal soft sediments, at the boundary Atlanticum/Subboreal around 5700 cal. yrs BP. This shift between *Micropsectra* and *S. coracina* has to some extent been described from north German lakes (Hofmann, 1971a). Hofmann discusses the impact of profundal oxygen concentration, stating that *Sergentia coracina* tolerates a lower oxygen saturation than *Micropsectra*, with minimum concentrations of 2 and 6 mg L^{-1}, respectively. This suggests that at Lake Stora Kroksjön, an increase in lake trophic status, reflected in lowered oxygen concentration, might have triggered the gradual decrease of *Micropsectra*. During the period where the taxa co-occur with similar frequencies (between 6000 and 4000 cal. yrs BP), LOI is approximately constant and the lake seems to have reached a maximum in productivity. Itkonen et al. (1999) and Seppä et al. (2002) both describe a positive correlation of *Sergentia* and organic sedimentation, and indeed, a strong correlation also exists at Lake Stora Kroksjön between *Sergentia* abundance and LOI ($r = 0.806, p < 0.01$). During the Subboreal, *Sergentia* outcompetes *Microtendipes*. Measurements taken irregularly at Lake Stora Kroksjön by the Blekinge Länstyrelsen show oxygen concentration of lower than 4 mg L^{-1} during the summer (July and August) in depths below 14 m (Figure III.5), supporting this interpretation. It also suggests that *Micropsectra* larvae may have had to migrate to the sublittoral, where oxygen concentration were sufficiently high for them to survive. There, water temperatures may have been above its optimum, so that the taxon was effectively squeezed into a narrow habitat between low oxygen concentrations below and high temperatures above. Additionally, longer transport of head capsules might have further reduced subfossil abundances, though Schmah (1993) says that the effect is negligible. In-

terestingly, other profundal species such as *Heterotrissocladius maeaeri* are commonly related to highly oxygenated profundal waters and do not decrease in such a distinct manner, suggesting strong competitive interactions between *M. insignilobus* and *S. coracina*.

An additional remarkable feature of the Late Subboreal (ca. 3900 cal. yrs BP) species assemblage is the immigration of *Mesocricotopus thienemanni*, a species with a very low temperature optimum in the Norwegian calibration set (Brooks and Birks, 2001). Not much is known about the ecological requirements of this species other than that it is classified as an inhabitant of the littoral and sublittoral of oligotrophic to mesotrophic lakes (Sæther, 1979; Wiederholm, 1983). Its presence may further support the interpretation of increasingly mesotrophic conditions under late-Holocene cooling.

The chironomid fauna of the Boreal to Subatlantic period are typical of the oligotrophic lakes of south Sweden, as described extensively by Brundin (1949), though he recorded higher species numbers (up to 140 species in contrast to a mean of 15 subfossil taxa). This can be due to the fact that the subfossil material cannot always be determined to the species level. Head capsules concentrations are generally low in comparison with Lake Lilla Torkelsjön and another Swedish lowland marl lake, where more than 100 head capsules were retrieved from 1 ml of wet sediment (Ferreri, 2003). The species diversity found in the samples was certainly influenced by low count numbers, even after correction by rarefaction. Generally, the lower species diversity in comparison with Lake Lilla Torkelsjön may be explained by the larger profundal habitat, which is less structurally complex and thus provides fewer niches for a diverse chironomid fauna.

1.4 The diatom record

Strong determinants identified for influencing diatom community composition in lakes (in the northern temperate and subarctic regions) include nutrient concentration (Hall and Smol, 1999), changes in lakewater pH (Renberg et al., 1993), salinity (Pienitz et al., 1995), and light- and habitat availability (Smol, 1988). Temperature plays a role as well, though the relationship between diatom distribution and temperature remains poorly understood ecologically (Bigler, 2001). A number of diatom-based transfer functions for temperature have been developed for high latitudes (Weckström et al., 1997; Rosén et al., 2000; Bigler and Hall, 2002) and altitudes (Lotter et al., 1997), and performance statistics are usually comparable to those based on other proxies as e.g., chironomids or pollen. Most of the calibration sets stem from remote areas where human impact on freshwater ecosystems has been low. Anthropogenic modification of the aforenamed factors is low in the calibration sets compared to Blekinge. Southern Sweden was inhabited and culturally altered by humans for several thousand years (Berglund, 1966b), thus freshwater ecosystems in the Blekinge area cannot be expected to have retained their pristine character. It is thus unlikely that a climate signal can be extracted from the diatom record. The qualitative interpretation of the diatom flora changes in Lake Stora Kroksjön is thus focused on hydrological, trophic and pH development.

The isolation of Lake Stora Kroksjön from the Baltic Ice Lake is reflected in the diatom flora. Prior to isolation, the numbers of diatom frustules were too low for analysis, likely reflecting both a low density of diatoms and the high sedimentation rate of BIL clays. The first sample allowing for closer analysis was 325 cm, with a modelled age of

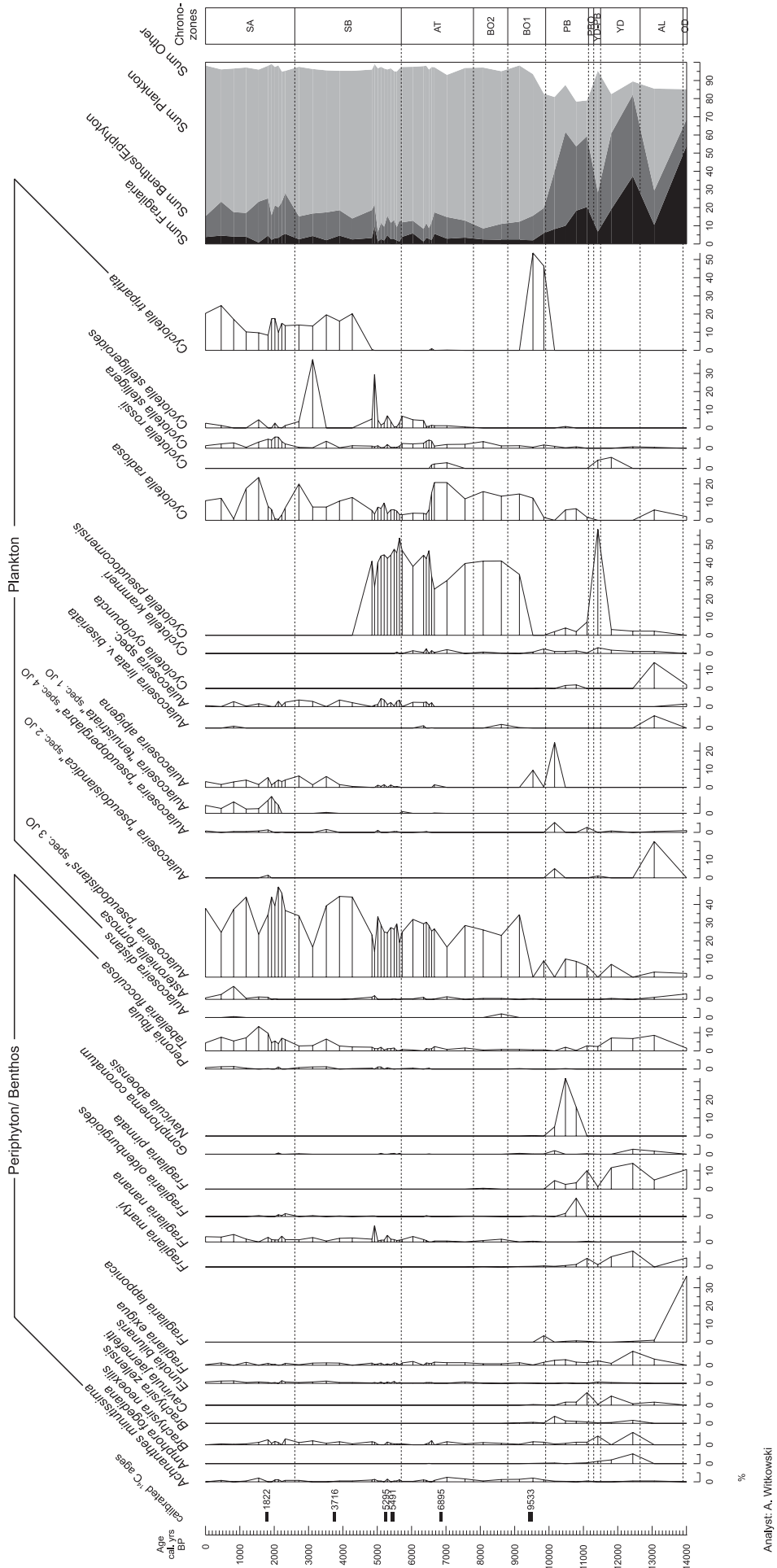


Figure VI.4: Percent abundance diagram of selected diatoms of Lake Stora Kroksjön depicting late-glacial and Holocene chronozones. Abbreviations: OD = Older Dryas, AL = Allerød, YD = Younger Dryas, PB = Preboreal, PBO = Preboreal Oscillation, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum. JO: Julma Ölkky, species sensu Lange-Bertalot and Metzelin (1996).

14,005 cal. yrs BP (Older Dryas). In this sample, the genus *Fragilaria* was the most abundant, along with species such as *F. pinnata, F. martyi, F. exigua*, and *F. lapponica* (see Figure V.19). *Fragilaria* is known as a pioneer genus, the small species of which are widely found in lake sediments from freshly deglaciated or isolated basins (e.g., Stabell, 1985; Smol, 1988; Bradshaw et al., 2000), tolerating poor light conditions (Anderson, 2000) in periods of high minerogenic input. In alpine lakes, *Fragilaria*-dominated diatom assemblages were found at the oligotrophic end of the TP gradient (Lotter et al., 1998).

The low number of sampled intervals covering the Allerød and Younger Dryas periods makes it difficult to make detailed statements about diatom flora development, but patterns are nevertheless detectable. The sample with an age of ca. 13,000 cal. yrs BP shows the first bloom of planktonic species, mainly of the genera *Aulacoseira* and *Cyclotella* (see Figure VI.4). In the two following samples which are of Younger Dryas age, benthic taxa dominate once more. The changes in life form likely reflect changes in length of ice-cover and the prevailing water-column mixing regime (Lotter and Bigler, 2000; Battarbee, 2000). For growth and reproduction, planktonic diatoms are dependent on sufficient mixing of the water column and are therefore hampered during periods of long ice-cover. Additionally, the low ratio of planktonic taxa may be due to high turbidity. Inwash of terrestrial minerogenic and organic material from unstable soils in spring, the critical time for diatom blooms, may have created turbid conditions that further restricted the development of phytoplankton. The unstable environmental conditions of the late-glacial and Holocene transition may have also favoured high species diversity during this period.

The distinct decrease in benthic and epiphytic species at the end of diatom zone SKRdia-1 (at the end of the Preboreal ca. 10,000 cal. yrs BP) is interpreted as the end of long winter ice-cover which led to the proliferation of planktonic diatoms. As the relative size of the benthic zone is small, the ratio of benthic to pelagic diatoms changed. Moreover, the increased catchment stability with a closed mixed forest vegetation (pollen zones SKR 4/SKR 5) probably led to less erosion in the catchment, lower turbidity, and thus to a higher light availability in the pelagial.

With the onset of the Boreal ca. 9900 cal. yrs BP (diatom zone SKRdia-2), a plankton-dominated diatom flora is established in Lake Stora Kroksjön. The most abundant taxa, *Aulacoseira 'pseudodistans'* sensu Lange-Bertalot and Metzelin (1996), *Cyclotella pseudocomensis* (probably a synonym of *Cyclotella comensis* (Scheffler and Morabito, 2003)), and *Cyclotella tripartita*, indicate oligo- to mesotrophic conditions. *Aulacoseira 'pseudodistans'* is like several other *Aulacoseira* species described from oligotrophic Lake Julma Ölkky, Finland (TP 4 μg L^{-1}, conductivity 17 μS cm^{-1}, Lange-Bertalot and Metzelin, 1996). In terms of trophy, the late-glacial and early Holocene diatom flora at Lake Stora Kroksjön seem to indicate more oligotrophic conditions than later in the stratigraphy. *Cyclotella comensis, C. radiosa* and *C. rossii*, abundant in SKRdia-3 which comprises the Late Boreal, Atlanticum and Early Subboreal periods, were found in lakes with mesotrophic conditions (Lotter et al., 1998).

The most significant change in the diatom species assemblage (characterising the boundary of zones SKRdia-3 and SKRdia-4) is the disappearance of *Cyclotella pseudocomensis* and the new establishment of *C. tripartita*, suggesting a strong ecological competition between these two species. Both species have been reported from oligotrophic conditions (Scheffler and Padisák,

1997; Scheffler and Morabito, 2003), but there are indications that *C. comensis*, to which *C. pseudocomensis* probably is a synonym, may be favoured by relatively high nitrate concentrations (Stoermer et al., 1996). The source of such relatively high nitrogen concentrations in the early Boreal may be related to the establishment of *Alnus*-stands at the lake shore (see Chapter VI.1.5). *Alnus* is capable of nitrogen fixation via fungal endosymbionts; its leaves can form a significant source of nitrogen for lakes, as they contain up to four times as much nitrogen as the leaves of other deciduous species (Wetzel, 2001). In Lake Stora Kroksjön, *Alnus*-pollen were first abundant in the sample dated to 9612 cal. yrs BP (242.5 cm), and a rise in *Cyclotella pseudocomensis* is noted in the second next sample (9137 cal. yrs BP; 232.5 cm). The time lag may be explained by a gradual accumulation of nitrogen in the water until it reached a threshold value allowing *C. pseudocomensis* to bloom. Additionally, coarseness of sampling may play a role. The source of high nitrogen concentrations possibly causing the first *C. pseudocomensis* peak is not as obvious. The abrupt disappearance of *C. pseudocomensis* from the diatom assemblage happened concurrently with a drop of *Alnus*-pollen from 22.5 to 14 %, and may be related to decreasing nitrogen input into the system, which gave *C. tripartita* a competitive advantage over *C. pseudocomensis*. However, when *Alnus*-pollen increased around 2700 cal. yrs BP, *C. pseudocomensis* did not bloom. Other environmental determinants may have suppressed a re-immigration into the system, or the other *Cyclotella*-species were more competitive during this period.

The diatom flora of Lake Stora Kroksjön includes no evident indicators of major changes in pH. The acidification caused by atmospheric deposition of strong acids from industrial air pollution is not captured by the uppermost sample of Lake Stora Kroksjön, probably because the uppermost layer was not retrieved by coring or because the temporal resolution is too small. Pre-industrial pH increases triggered by human land-use as described by Renberg et al. (1993), is not detected easily, though the increase in *Asterionella formosa* in zone SKRdia-4 may be a signal related to the effect in question.

A distinct feature of the diatom flora of Lake Stora Kroksjön is the exceptionally high number of taxa present through time; 344 taxa were identified and the overall number of species present may well exceed 500 (A. Witkowski, pers. communication). High diatom species numbers have been shown to be a feature of oligotrophic freshwater environments (Lange-Bertalot and Metzelin, 1996). The phenomenon has been tentatively interpreted as a result of an effective buffering of lake water pH by humic acids in soft water lakes, that allows for oligotraphent species sensitive to acidification to thrive (Lange-Bertalot and Metzelin, 1996). Decreasing species numbers and diversity at the end of the late-glacial period (Figure V.20a and b) may be related to an increasing lake trophy. This supports the interpretation of Lake Stora Kroksjön to have moved from an oligotrophic to a mesotrophic system, as suggested by the chironomid stratigraphy. However, diatom species diversity was very stable from ca. 10,000 cal. yrs BP on.

1.5 Vegetation history

From the late-glacial, vegetation development has been controlled by climate, soil, and disturbance. Climate is a key factor controlling the development of a plant community by length of growing season, temperature and precipitation. Together with soil conditions and - becoming more and more important in the later part of the Holocene - human impact, these fac-

tors have determined the nature of the terrestrial plant communities present at Lake Stora Kroksjön.

Vegetation history inferred from pollen records has to take into account the size of the area from which pollen have been transported to the site where they were finally deposited. Some pollen types, especially airborne ones like *Quercus* or *Pinus*, can be transported over more than 100 km, and deposition is dependent on basin size and shelter (Prentice, 1985; Sugita, 1994). A 50 km radius of the 'relevant pollen source area' has proved as a good compromise for small (250 m radius) lakes when all pollen types are considered together (Lindbladh et al., 2000). With the surface area of Lakes Stora Kroksjön and Lilla Torkelsjön being larger than that, a regional rather than local perspective of the vegetation history is described.

Allerød and Younger Dryas; 14,000–11,500 cal. yrs BP

The time when vegetation development and dynamics were highest, i.e., when vegetation was not in equilibrium with climate immediately after deglaciation and until the early Holocene, is only represented by a few samples in Lake Stora Kroksjön. During this period, the freshly deglaciated, barren landscape without top soils developed from pioneering vegetation cover to park tundra to a woodland landscape (Berglund et al., 1994). These processes are poorly captured by the pollen analysis, especially in the first zone when only three samples cover, according to the age-depth model, the time span of Older Dryas, Allerød and Younger Dryas. In this zone, *Pinus*-pollen are dominant, but probably only because of long-distance transport. The high amounts of *Artemisia*, Chenopodiaceae and Poaceae pollen emphasise the tundra character. For the Blekinge region, Berglund (1966a) describes a rather open birch forest with scattered pines in more sheltered stands during the Allerød, with abundant shrub and dwarf-shrub vegetation (*Salix*, *Betula nana*, *Empetrum nigrum*, and *Juniperus*). The open, woodless tundra landscape of the Younger Dryas seems to be reflected most faithfully by the pollen composition of sample 315 cm because of the low pollen count sums, low tree pollen numbers and high amounts of herb pollen. The age-depth model places this sample into the Allerød. Overall, the late-glacial vegetation dynamics can not be accurately characterised in the pollen record, but the main features are similar to those so thoroughly described by Berglund (1966a) for eastern Blekinge.

Directly after deglaciation, the humus-poor, unstable mineral soils were colonised by a pioneering herb vegetation consisting of plants with low competitive power, plants characteristic of soils rich in mineral nutrients and demanding abundant light. Among these, *Artemisia* spp., *Dryas octopetala*, *Hippophaë rhamnoides*, and *Saxifraga oppositifolia* were common. The areas that had already become icefree and where soils had developed were covered with a dwarf shrub vegetation of *Betula nana* and *Salix*. During the climate amelioration of the Allerød chronozone, a subarctic mixed forest with *Betula pubescens* dominated. *Pinus* stands may have been present on well-drained soils. The dwarf-birch and willow shrub heaths were enriched by *Empetrum*, and open *Artemisia*-grass communities covered smaller areas due to forest expansion. The cold Younger Dryas put a halt to forest expansion and the vegetation became essentially treeless. *Juniperus*, *Betula nana*, and *Salix* were common and the dominating vegetation plant community was *Artemisia*-grass vegetation.

Preboreal; 11,500–9900 cal. yrs BP

With the end of the Younger Dryas cold event, the climate conditions were more subarctic than arctic, and arctic and alpine flo-

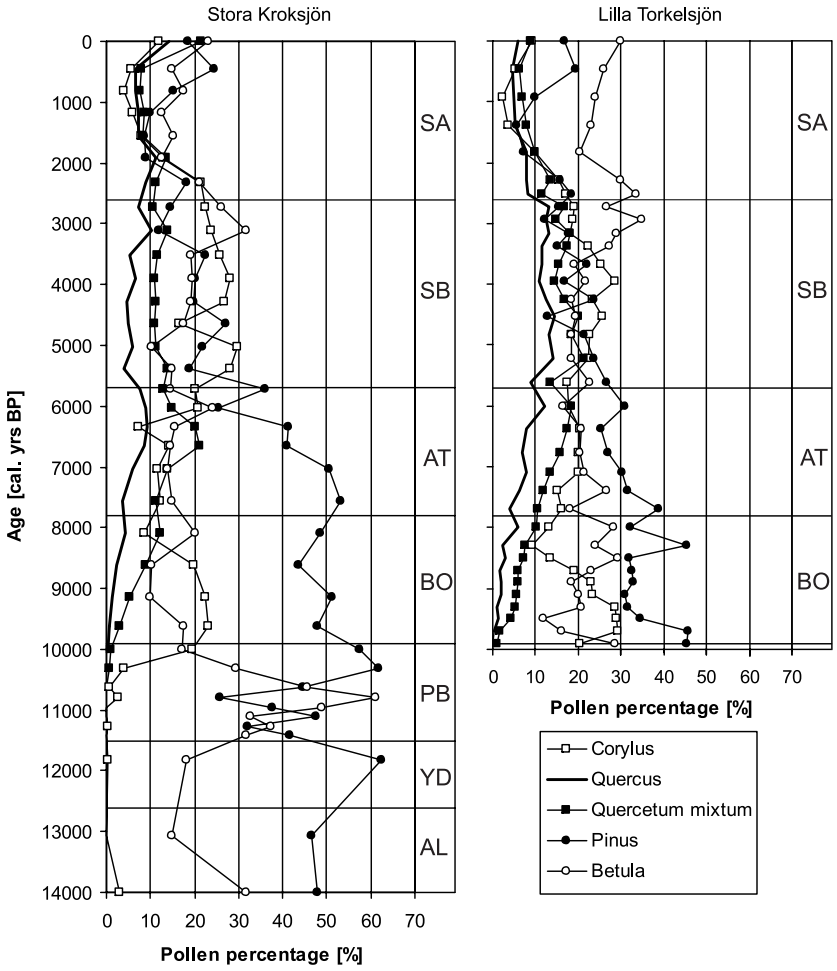


Figure VI.5: Percentage diagram of selected pollen types at Stora Kroksjön (left) and Lilla Torkelsjön (right). Quercetum mixtum: $\sum$ of the *Quercus, Tilia, Fraxinus* and *Ulmus* pollen types. Abbreviations: AL = Allerød, YD = Younger Dryas, PB = Preboreal, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum.

ral elements decreased. The YD-PB transition period, as well as the whole Preboreal, is characterised by rising pollen counts, and especially rising tree pollen abundance. *Betula pubescens* and *Pinus silvestris* were the dominant tree species. This period is captured by three pollen zones, SKR2, SKR3 and SKR4, that reflect the forest succession. Directly at the end of the Younger Dryas, during the YD-PB transitional period, increases in *Betula*-pollen mark the development of birch forest much like it was present during the Allerød. With the closing of the forest canopy, the long-distance deposition of *Pinus*-pollen decreased and thus *Pinus* abundance appears to decline during this time. This process is shortly reversed during the short climate deterioration of the Preboreal Oscillation (PBO), which is clearly depicted in the first sample of zone SKR3 (see Figure VI.3), by a plateau in LOI and low pollen counts. The coincident increase of herb pollen seems quite unusual compared to other regional records and may be of local significance only. The remainder of the Preboreal is divided in two subperiods as described in Berglund (1966a). 'Subperiod a' (comparable to zone SKR3) is marked by the

strong *Betula* expansion, supposedly due to the immigration and rapid spread of *Betula verrucosa*. *Juniperus*, dependent on good light conditions in open forest but temperate climate, has a maximum in the not yet too densely forested landscape, as does *Calluna*. Open communities with *Empetrum nigrum*, *Chenopodiaceae* and *Salix* were still quite common, but in the 'Subperiod b' (comparable to zone SKR4) disappeared or became restricted to very small areas. In 'Subperiod b', the vegetation developed to a mixed pine-birch forest and late-glacial open vegetation types were almost non-existent. Forest development in the Preboreal implies subarctic to cool-temperate climate conditions that warmed considerably. The first broad-leaved tree, *Ulmus*, immigrated into Blekinge at this time.

Generally, the vegetation of the glacial and early post-glacial periods is distinctly different from the rest of the Holocene, as the dendrogram in Figure V.24 shows, likely with the absence and presence of deciduous forest as the segregating feature.

Boreal; 9900–7800 cal. yrs BP

The Boreal began with the immigration of *Corylus*, the first shade-tolerant shrub of the post-glacial forest vegetation. The boundary of the chronozones Preboreal and early Boreal (PB/BO1; ca. 9900 cal. yrs BP) seems not to be entirely synchronous with the LPAZ boundary between SKR4 and SKR5. This is due to the increase of *Corylus* in the 255 cm sample ($\cong$ 10,000 cal. yrs BP), which places the zone boundary between this and the previous sample, and thus markedly earlier because of the coarse sampling intervals (see Figure V.24 and VI.5). *Pinus* became the main forest tree, and *Corylus* probably succeeded *Betula*. The forest vegetation became more species-rich with the immigration of broad-leaved trees, such as *Quercus* and *Ulmus* in the early Boreal and *Tilia, Acer*, and *Fraxinus* in the late Boreal. Even though *Acer*-pollen were not found in Lake Stora Kroksjön, the species was probably present, but it is not possible to determine the time of its immigration. *Acer*-pollen are, as a rule, found only in very low proportions due to its entomophilous reproduction modus together with low pollen production. The above-named trees were common on well-drained dry soils, whereas in places with high water level such as lake shores, *Salix* was replaced by *Alnus*. The early immigration and high values of *Alnus* pollen as found in both Lakes Stora Kroksjön and Lilla Torkelsjön are more typical for the oceanic climate of southwestern Sweden (Skåne, in English Scania) and were never found in eastern Blekinge (Berglund, 1966b). This indicates that western Blekinge, in terms of increasing continentality, has an intermediate position between Skåne and eastern Blekinge.

The boundary characteristics of BO1/BO2 (ca. 8800 cal. yrs BP) as described by Berglund (1966b) for eastern Blekinge (the rational *Alnus* and *Ulmus* limits) are found earlier, in zone SKR5. This boundary is possibly metachronous and does not depict a climatological but rather a successional boundary. As the vegetation development of Denmark and Skåne differs from that of eastern Blekinge, the study sites may lie on a transitional zone between these floral elements and *Alnus* and *Ulmus* may have immigrated earlier than in the eastern part of Blekinge. At the end of the Boreal period, *Pinus*-dominated forests were still common, but the initially slow successive replacement of pine forest by *Corylus, Quercus, Ulmus, Tilia* and *Fraxinus* gained momentum. Woodless communities with *Calluna, Juniperus* and *Artemisia* had become rare and existed probably only as fragmentary heaths in rocky areas or at the shores of lakes and the Baltic. The immigration of southern species indicates higher temperatures than earlier. Indications of a drier cli-

mate, or lowered groundwater levels during this time, as reported from several sources (cited in Berglund, 1966b), are not present.

Atlanticum; 7800–5700 cal. yrs BP
The boundary of the Atlanticum chronozone as described from eastern Blekinge is not easily discernible at Lake Stora Kroksjön. It comprises the zones SKR6, SKR7 and the lower part of SKR8 (see Figures V.24 and V.26). Berglund (1966b) suggests the most prominent feature of this period is the rise of the *Tilia*-curve and a general rise of the so-called *Quercetum mixtum* pollen, the sum of *Quercus, Fraxinus, Tilia* and *Ulmus* pollen percentages. These features are already clearly visible in the two samples constituting zone SKR6 (Figure V.24 and Figure VI.5) (the placement of the zone boundary in the middle between two samples dated some 600 years apart makes the transition older than it should be). The boundary between the early and late Atlanticum periods, mainly characterised by the rise of the *Quercetum mixtum*, due to an increase of *Quercus*-pollen, can be placed between the samples dated at 7027 and 6661 cal. yrs BP. Concurrently, the *Pinus*-curve falls, reflecting a change between different communities. Whereas in the early Atlanticum, the pine forests dominated the western Blekinge region, a regression in favour of broad-leaved trees occurred in the transition between the two subperiods. The rise of *Corylus* in zone SKR8 is a feature Lake Stora Kroksjön has in common with the Late Atlanticum period of Skåne and Denmark, and emphasises once again that western Blekinge, in terms of vegetational development, is more closely related to those regions than to eastern Blekinge. The vegetation indicates that the climate was warm and humid.

There are no clear signs of human impact on the vegetation. Archeological evidence shows that Blekinge was colonised from west to east during the Late Mesolithic time (≅ Late Atlanticum, see Chapter IV.3) by the Ertebölle culture. These Mesolithic people were fishers and hunters and lived primarily near the coast (Berglund, 1966b).

Subboreal; 5700–ca. 2600 cal. yrs BP
The lower boundary of the Subboreal period is marked by a decrease in *Ulmus* from around 7 to 1.5 %, known as the 'elm decline' ('Ulmenfall'). This event is captured within the pollen zone SKR8, in the sample dated at 5730 cal. yrs BP (152.5 cm). This sample also incorporates other features of the boundary described by Berglund (1966b), e.g., minima of *Ulmus, Tilia, Fraxinus* and *Quercus* corresponding with a *Pinus* maximum. The first signs of human influence of the vegetation are seen with the increase of *Filipendula*, *Plantago lanceolata*, *Rumex acetosa/acetosella*, and undifferentiated Poaceae pollen types, indicating forest clearing and land use (Gaillard et al., 1996). The 'elm decline' is a phenomenon probably caused by a complex of interacting factors, among them the outbreak of elm disease, sudden climate change, soil leaching, followed by increased human impact (e.g., Troels-Smith, 1960; Iversen, 1973; Birks, 1986; Berglund, 1991a). The climate change was mainly from oceanic to more continental conditions (Berglund, 1966b), bringing about colder winters and warmer, drier summers. Increased continentality can be seen in the climate indicators *Hedera* (ivy) and *Viscum* (mistletoe), which decrease substantially at the Atlanticum/Subboreal transition. Both pollen types occur in the sediments of Lake Stora Kroksjön, but not to a great extent. The main vegetation type was a broad-leaved forest, similar to that which grew during the Atlanticum, however, human influence in the vegetation became more noticeable. During the Neolithic phase (≅ Early Subboreal), human impact on the vegetation in Skåne was caused by small-scale farming (Berglund, 1991a). The so-called slash-and-burn technique cultivated

burned tree cuttings for some years before leaving them to forest regeneration. On a small scale, stock-raising on wood pastures was also practiced. The woods were coppiced as a source for building material and to obtain leaf fodder. Within the coppiced areas, fast-growing shrubs like *Corylus* and grass and herbs were favoured. These practices were likely present in Blekinge, but to a lesser extent than in Skåne.

The boundary of early to late Subboreal (ca. 3750 cal. yrs BP), characterised by the increase of *Carpinus*, an expansion of *Betula* and a decrease of the *Quercetum mixtum* forest, of which the latter is not obvious at Lake Stora Kroksjön (Figure VI.5), is seen in the boundary between SKR9 and SKR10. The increase of human influence at this time is mainly evident by the increase in non-arboreal pollen. The expansion of *Betula* in the later part of the late Subboreal, which replaced the original broad-leaved forest vegetation, was probably caused by a gradual change in climate and edaphic conditions. Lower summer temperatures, increased humidity and soil leaching led to a decline in meadow forest with shade-tolerant species favouring heath forest with birch (Berglund, 1966b, 1991b). *Fagus* and *Carpinus* immigrated into the area from Denmark and Skåne.

Subatlanticum; ca. 2600–0 cal. yrs BP
The most drastic forest community change at Lake Stora Kroksjön since the end of the Pleistocene is recorded at the boundary of the Subboreal and the Subatlanticum (estimated ca. 2600 cal. yrs BP). This is coincident with the boundary between zones SKR10 and SKR11. *Fagus*-pollen were found considerably earlier in the Holocene in zone SKR8 (5000 cal. yrs BP), but a massive expansion occurred at this boundary. The regionally and temporally incoherent establishment of *Fagus* in southern Sweden suggests that climate was not the (only) limiting factor driving this development, but that human disturbance may have played an important role (Björkman, 1999). *Fagus* seeds are highly dependent on ground disturbance for successful establishment (van Röhrig et al., 1978), suggesting that forest disturbance had occurred around Lake Stora Kroksjön. However, pollen source areas may well be as far as 10–30 km away. Additionally, since measures of human-impact indicators (sum of Poaceae and *Plantago lanceolata* for meadows, sum of *Juniperus* and *Calluna* for pasture and sum of Poaceae > 40 μm and *Rumex acetosa/R. acetosella* for cultivated land) are low compared to those of Björkman (1999), it seems that severe forest disturbance by clearance and cultivation had not taken place in the direct vicinity of the lake. On the other hand, forest grazing of domestic animals, especially by pigs, may have contributed to the spread of beech forest at the site or south of it, closer to the coast.

Fagus-pollen reach maximum values in the middle of the Subatlanticum, between 1550 and 1200 cal. yrs BP (4th to 7th century) in accordance with other South Swedish records (e.g., Berglund, 1966b; Digerfeldt, 1972; 1974; Björkman, 1996; Lindbladh et al., 2000). Thereafter, *Fagus* percentage decreased in favour of *Betula, Pinus, Corylus* and terrestrial herbs, all pointing towards increasing human impact. Forest clearance, wood utilisation for building, and burning and forest grazing have increased since the Medieval period. However, the uppermost sample shows a distinct increase in broad-leaved forest tree species.

The effects of very recent climate developments, such as the Medieval climate maximum or the Little Ice Age are not evident neither at Lake Stora Kroksjön nor at Lake Lilla Torkelsjön, though the Little Ice Age may have been the event with the highest amplitude since the beginning of

the Holocene (Williams and Wigley, 1983). Lindbladh et al. (2000) state that recent model-based analysis of forest dynamics during the last 1000 years have shown that climatic changes were often similar to, and thus concealed by, overriding anthropogenic effects. It seems that both climate deterioration and anthropogenic activity result in reduction of total forest biomass and a reduction of the importance of deciduous trees.

Immigration of *Picea abies* in the direct vicinity of Lake Stora Kroksjön seems not or only to have occurred in very small amounts, though it is today abundant at Lake Lilla Torkelsjön, only 5 km distant. The lake lies directly on the southern limit of the *Picea* forest (Lindquist, 1959), which has moved southward during the last centuries due to cultural activities (Berglund, 1966b; Björkman and Bradshaw, 1996). In a forest survey from 1684 cited in Berglund (1966b), spruce was only recorded at two sites in the whole province of Blekinge.

1.6 Climate reconstruction

When considering the results of the Holocene temperature reconstruction, one has to bear in mind that the sample resolution is relatively coarse and the sample-specific prediction errors are large (±1 °C) compared with the magnitude of Holocene temperature changes in Scandinavia (±1.2–2.7° C, e.g., Dahl and Nesje (1996); Rosén et al. (2001); Seppä and Birks (2002); Korhola et al. (2002); Bigler et al. (2003)).

The chironomid-inferred summer temperatures, ranging between 10–13 °C, seem low for a reconstruction at lower latitudes. Other chironomid-based temperature reconstructions infer rather similar values at high-latitude Lappish (Bigler et al., 2002; Korhola et al., 2002; Rosén et al., 2001) or Swiss alpine (Heiri et al., 2003a) sites. The fact that all these sites lie at considerably higher altitudes than Lake Stora Kroksjön suggests that the absolute values of the reconstructed temperature are too low. Temperature lapse rates with increasing altitude are estimated to 0.6 °C per 100 m altitude (Laaksonen, 1976; Livingstone et al., 1999). Comparison with present-day temperatures at Lake Stora Kroksjön give further evidence that the reconstructed values may be too low. The topmost sample, modelled to represent present-day conditions, inferred 11.8 °C. The current mean July air temperature is 16.3 °C measured at a weather station 7.5 km north (Grimsmåla, SMHI station Nr. 6420). The discrepancy of 4.5 °C may be derived from several factors.

1. The applicability of the model is limited by the span of the temperature gradient. The warmest mean July air temperature incorporated in the model is 16 °C, whereas nowadays temperature at the closest weather station is 16.3 °C.

2. The southernmost site sampled for the Norwegian calibration set lies about 250 km north of the study site, and the warmest site had a mean July temperature of 16 °C. Possibly, the applicability of the model may, though taxonomic overlap seems great and the general ecological nature of the sample sites are comparable, still be limited by geographic differences.

3. The oceanic climate conditions in Norway may allow a similar species assemblage to live at lower mean summer temperatures than at Blekinge, if milder winter conditions allow for an earlier ice break and rise of water temperature in spring. Thus, the same species assemblage may underestimate summer temperatures at a more continental site.

4. The size and depth of Lake Stora Kroksjön may result in an over-representation of profundal taxa, which through the stable summer stratification remain more isolated from direct climatic effects than the littoral fauna. Temperature change exerts stronger effects on the latter, but Weighted Average (WA) models are largely driven by the dominant taxa in a system. However, profundal taxa may be less powerful indicators for climate, as they often occur over the whole length of the gradient, inhabiting the profundal of lakes in the temperate regions but the littoral of high-latitude sites. Their modelled temperature optimum may thus be pulled from the cold end towards the center of the gradient.

5. Even though taxonomic consistency was carefully assessed, errors in species determination may have occurred. Additionally, since it is sometimes difficult to discern subfossil chironomid head capsules on species level, subfossil material determined to genus level may include different species with different temperature optima. However, temperature reconstruction based on chironomid genera has shown to be robust even in intercontinental comparison (Lotter et al., 1999)

6. Additionally, a low pH may have similar effects on the midge community as low temperatures (Brodin and Gransberg, 1993; Schnell and Willassen, 1996). However, decreasing pH trends are not detected among the diatom community of Lake Stora Kroksjön and it seems that pH has had little influence on the dynamics of the chironomid assemblage.

7. The quality of present day temperature data may differ from the temperature data used in the Norwegian calibration set. In Norway, the 30 year mean of 10–20 weather stations was used. The present day data in Sweden is derived from only one station and its accuracy could not be checked.

The reliability of the reconstruction is not exactly the same for every sample. During the whole sequence, nine of 44 samples had no good analogues within the calibration data set. These were mostly samples with fewer than 80 head capsules. The fact that only one taxon of the fossil data did not occur in the calibration set (*Conchapelopia*, 0.12 % overall occurrence, 3.6 % maximum occurrence in a sample) suggests that the bad analogue situation was produced by uncommon percent abundances resulting from low count sums rather than by a chironomid species assemblage not present in modern lakes. The 270 cm sample (10,477 cal. yrs BP) was the only sample which had a high head capsule count sum (n = 113) and was not well represented in the calibration set. This was probably due to the uncommonly high representation (> 50 %) of *Micropsectra insignilobus* gr. that has no equivalent in the calibration set (Brooks and Birks, 2001). Thus, even though some samples show poor analogues in relation to modern chironomid assemblages, it is expected that the reconstruction provides reasonable temperature trends for the whole sequence. Additionally, WA-PLS performs reasonably well even under sub-optimal analogue conditions (Birks, 1995).

Despite the preceding shortcomings, the long-term temperature reconstruction trends are in good accordance with the pattern of climate change during late-glacial and Holocene in Europe, as e.g., reconstructed from the GRIP ice core borehole (Dahl-Jensen et al., 1998), from glacier margin movements (Nesje and Kvamme, 1991) and

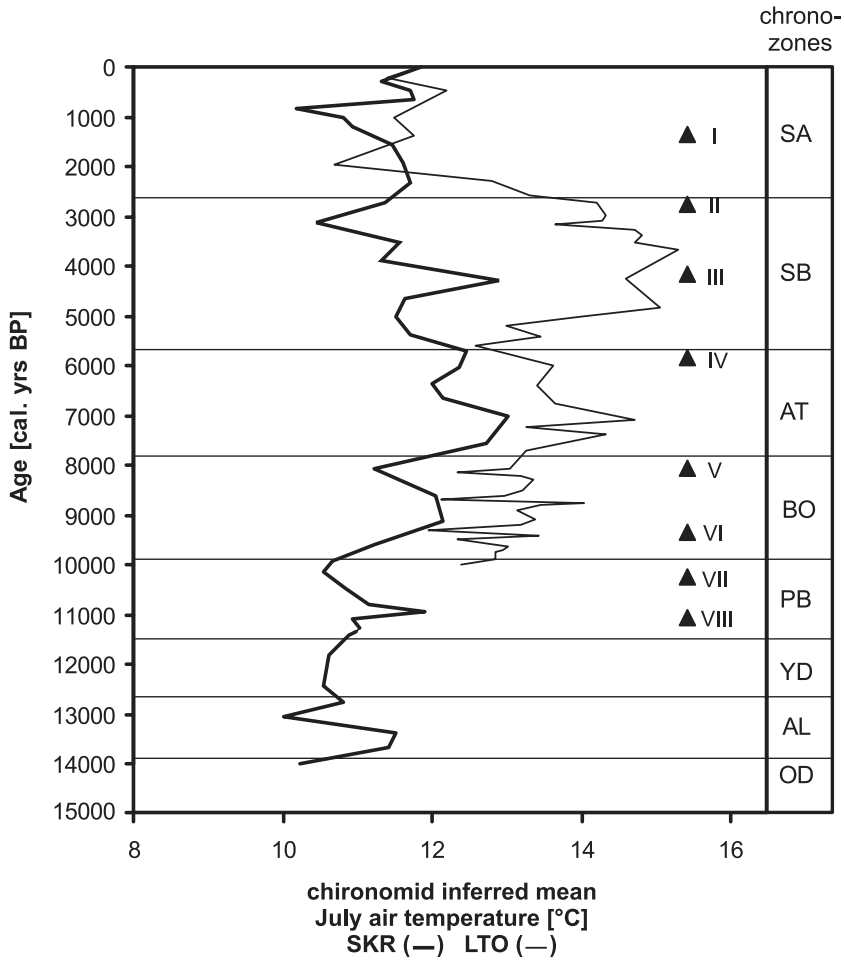


Figure VI.6: Chironomid-inferred mean July air temperatures at Lakes Stora Kroksjön and Lilla Torkelsjön in comparison to ice-rafting events reported from North Atlantic sediments (Bond et al.,1997, triangles). The events were dated to 1400 (I), 2800 (II), 4200 (III), 5900 (IV), 8100 (V), 9400 (VI), 10,300 (VII) and 11,100 (VIII) cal. yrs BP.

from pollen (Seppä and Birks, 2002): After the initial warming at the end of the Pleistocene, increasing temperatures led to a mid-Holocene thermal maximum (ca. 8000–6000 cal. yrs BP), when mean inferred temperatures were about 1 °C above present day values. Subsequently, a cooling trend occurred and cooler conditions are inferred from the species assemblage for the Late Holocene. In the following, the reconstruction is examined in detail.

Even though the analogue situation in the late-glacial sequence is not satisfactory, general climatic trends affected the chironomid community and are reflected in the temperature reconstruction. However, it is questionable if the magnitude of climate variation is reproduced correctly. The temperature drop during the short Gerzensee oscillation GRIP-event GI-1b) is with ca. 1.5 °C greater than that of the Younger Dryas event. The Younger Dryas, though strongly reflected in species compositional change (e.g., the marked decrease of littoral taxa), does not infer as pronounced temperature drops as other chironomid-inferred Younger Dryas-temperatures from e.g., western Norway (ca.

2.5 °C, Brooks and Birks, 2001) or Scotland (ca. 2.2 °C, Brooks and Birks, 2000b). This is due to the fact that here, the temperature reconstruction is largely driven by the profundal community. Among the profundal taxa, *M. insignilobus* gr. has a lower temperature optimum within the Norwegian calibration set than for example, *H. grimshawi*. Other ecological factors making the latter taxon such good competitor at Lake Stora Kroksjön during the Younger Dryas are obviously more important than temperature. The presence of cool conditions during this period, that should actually favour *M. insignilobus* gr., are reflected in other proxies, e.g., low head capsule counts, the composition of the surrounding vegetation, pollen productivity and organic sedimentation (LOI).

During the Younger Dryas-Preboreal transition period, inferred temperatures remain cool (Figure VI.3). The Preboreal oscillation (PBO, 11,300–11,150 cal. yrs BP) seems to be captured by the sample with a modelled age of 11,107 cal. yrs BP (290 cm) in terms of LOI and vegetational parameters, even though the temperature drop is well within the model error. Another prominent temperature drop comprises the samples dated 10,162 and 9926 cal. yrs BP (260 and 252.5 cm), that infer lower values than the Younger Dryas samples. This temperature minimum is in good agreement with a cool event reported from Western Scandinavia (the so-called Erdalen event, Nesje and Dahl, 1994, Matthews et al., 2000) as well as from Central Europe (e.g., Haas et al., 1998, estimated to 10,300 (Norway) and between 10,750 and 10,200 (Central Europe)). The decrease in summer temperatures has been estimated to 0.8 °C (Haas et al., 1998), which agrees well with the temperature reconstruction, which suggests a temperature decline of 0.9 °C between 10,800 and 10,150 cal. yrs BP. Bond et al. (1997) present evidence for cyclic enhanced ice-rafting events in the North Atlantic that caused sea surface cooling and subsequently changes in the ocean circulation. Event number VII is dated to 10,300 cal. yrs BP (Figure VI.6).

With the onset of the Boreal and for the entire Early Holocene, the chironomid assemblage infers warming climate conditions (Figure V.13), ranging between 12 and 13 °C. Maximum temperatures are registered the end of the Atlanticum. The sample at 212.5 cm (8082 cal. yrs BP) infers a distinctly cooler temperature and is in good temporal agreement with the widespread cold event in the Northern Hemisphere centered around 8200 cal. yrs BP (Alley et al., 1997; Bond et al., 1997 event V), the magnitude of which is estimated to be a drop of 1.7 °C mean annual temperature in southern Germany (von Grafenstein et al., 1998). At Lake Stora Kroksjön, a temperature drop of about 0.8 °C occurs. On a species community level, this drop is reflected by a peak in the abundance of the cold-adapted and oxygen-demanding *M. insignilobus* gr..

After the cooling around 8200 cal. yrs BP, inferred temperatures rise about 1 °C and reach their Holocene maximum in good temporal accordance with the general climate trends reconstructed in the Nordic regions, even though there is some discrepancy in the exact timing of the thermal optimum when comparing different reports from North Scandinavia. While Bigler et al. (2003) (diatoms and chironomids) report the warmest conditions from the early Holocene prior to 8000 cal. yrs BP, Dahl and Nesje (1996) (glacier equilibrium-line altitude), Seppä and Birks (2002) (pollen), Korhola et al. (2002) (chironomids) and Rosén et al. (2001) (multiple proxies) have inferred warmest temperatures after 8000 cal. yrs BP, which correspond with the results at Lake Stora Kroksjön. In all reports, the thermal optimum is calculated to have been between 1.2 and 2.7 °C warmer than present day

values. At Lake Stora Kroksjön, maximum Holocene temperatures lie 1.2 °C above the sample representing present day conditions. However, since the temperature reconstruction at Lake Stora Kroksjön does not reproduce present day values correctly, the magnitude of Holocene temperature change may be underestimated. Climate variability may have been large during the Holocene, and it is therefore possible that climate change was less pronounced in southern Sweden than in the north.

A general cooling trend is inferred from ca. 5700 cal. yrs BP to the boundary with the Subboreal. It reflects the start of a general late Holocene cooling in the northern hemisphere, accompanied by glacier re-advances in Norway (Dahl and Nesje, 1996; Nesje and Kvamme, 1991), a lowering of tree-line in northern Sweden (Kullman, 1995) and the southward retreat of tree-line in Northern Fennoscandia (Karlén, 1976; Kullman, 1995; Seppä and Weckström, 1999). The mean summer temperatures lay around 11.5 °C. Three data points falling into the period between 1200 and 820 cal. yrs BP (AD 750–1130) stand out from the general downward trend in inferring temperatures that drop as low as 10.2 °C, which is only 0.2 °higher than the coldest inferred temperature in the Younger Dryas. This is in good agreement with the findings of Matthews et al. (2000), who report a period of advancing glaciers between 1400 and 800 cal. yrs BP (AD 550–1150) in south-central Norway, but do not confirm a Medieval Warm Period centered around AD 1000 (950 cal. yrs BP; Dahl-Jensen et al., 1998). As these samples had no analogues in the Norwegian calibration set due to low headcapsule counts and may therefore produce unreliable values, a careful re-investigation of these samples would perhaps bring forward different results. There is no clear evidence for the climate deterioration called the 'Little Ice Age' (LIA), but there is a 0.5 °C drop in the sample dated 270 cal. yrts BP (AD 1680). The LIA's duration is estimated as roughly between AD 1200–1850 (Karlén, 1976; Dahl-Jensen et al., 1998; Lockwood, 2001; Nesje and Dahl, 2003), but adjacent samples at Lake Stora Kroksjön do not show strong deviation from the 'baseline' temperature of the late Holocene.

The chironomid-inferred late glacial and Holocene temperatures at Lake Stora Kroksjön are in good agreement with the temperature trends established for northern Europe. Though the absolute inferred values are probably too low by 1–2 °C, the qualitative course likely reflects the regional climate development during the Holocene.

1.7 Lake Stora Kroksjön Synthesis

The synthesis of subfossil chironomid, diatom, pollen and sediment characteristic analyses at Lake Stora Kroksjön reveals how the lake system and its catchment has changed over time since the last deglaciation. Directly after deglaciation, when Lake Stora Kroksjön was part of the Baltic Ice Lake, the lack of fossil material indicates rather hostile life conditions in the cold, debris-rich water. As the lake basin lies close to the highest coastline, it can be envisioned as an embayment of the BIL with high wave action. Only very few remains of the freshwater biocoenosis were found from this time. The low numbers of fossil remains are probably also due to the highly energetic sedimentary environment that may have destroyed fossils. The high sedimentation rates additionally diluted the concentration of floral and faunal remains in the sediments. The few remains that have been found point towards a cold freshwater environment.

Since its isolation from the BIL ca. 14,000 years ago, during the Older Dryas cold event,

Lake Stora Kroksjön has been a typical Scandinavian oligo- to mesotrophic lake that has in terms of limnology not undergone drastic changes. However, gradual or abrupt changes in some species assemblages have occurred and are documented in this thesis. Nearly concurrent with the isolation from the BIL, more favorable climate conditions set in with the Allerød warm period and Lake Stora Kroksjön was quickly colonised; species diversity of the midge fauna and diatom flora was high. The crustaceans *Mysis relicta*, *Monoporeia affinis* and *Pallasea quadrispinosa*, inhabitants of the BIL, remained in Lake Stora Kroksjön when it became isolated and have since remained part of the fauna (Kinsten, 2003).

Though during early Allerød limnic productivity increased, a stagnation is registered the in late Allerød, following the Gerzensee Oscillation. The concentration of midge headcapsules decreased markedly and the LOI remained stagnant. However, the number of samples covering this period are low in all indicators and the late Allerød is especially poorly represented. It can, however, be assumed that climate conditions were generally favourable and the Gerzensee Oscillation was only a short interruption.

In contrast, the Younger Dryas brought about strong changes in lake and catchment ecology. Pronounced changes among chironomid, diatom, and vegetation remains clearly document the recurrence of glacial conditions. Among the chironomids, cold-stenothermic taxa dominated the assemblage. Within the diatom flora, benthic and epiphytic ecotypes dominated, due to prolonged ice-cover. High percentages of herb and shrub pollen document the tundra character of the vegetation in the lake catchment. The LOI remained low, reflecting low lake productivity.

The end of the Younger Dryas stadial was correlated with other sites in Blekinge, described by Berglund (1966a) and Björck (1979) as increases in LOI and arboreal vegetation. Even though lake productivity started to increase ca. 10,500 cal. yrs BP, climate conditions remained rather cool until the end of the Erdalen event, around 10,200 cal. yrs BP. The low chironomid-inferred temperatures for this event are supported by the high proportion of benthic diatoms until ca. 10,150 cal. yrs BP, documenting prolonged ice-cover.

The onset of warm climate conditions at the end of the Preboreal are mirrored by a strong rise in lake productivity, with carbon content rising now distinctly above 25 %. Some cold-adapted midge-species disappeared from the lake, while others decreased in numbers. Warm-adapted species immigrated and became established in considerable numbers. Within the diatom assemblage, the change in climate is mainly documented by the dominance of planktonic forms, which now found a suitable mixing regime in the lake.

With the onset of the Subboreal chronozone, a mean drop of summer temperatures of about 1 °C, to around 11.5 °C, was inferred. The coldest Holocene temperatures were inferred during the Subatlanticum, which is in accordance with the opinion that the global climate fluctuations during the last 1500 years have been among the most extreme experienced during the entire Holocene (Williams and Wigley, 1983). A distinct temperature minimum occurred around 1000 cal. yrs BP, which had no equivalent at Lake Lilla Torkelsjön. However, chronological errors may have arisen from the assumption that the uppermost sample represents present day and the signal may really be related to Bond's (1997) 1400 cal. yrs BP ice-rafting event.

During the Boreal and Atlanticum, midges and diatoms indicate a cool, oligotrophic

deep lake environment with abundant oxygen in the profundal. The carbon sedimentation was slowly increasing until maximum LOI values were reached in the Atlanticum, around 6800 cal. yrs BP, and remain high for the rest of the sequence. From ca. 5600 cal. yrs BP, mild oxygen depletion in the profundal zone occurred, indicated by the chironomid assemblage, which is interpreted as a sign of increased lake productivity. However, changes in diatom composition hint towards a reduced nitrogen load of the water between 4600 and 4200 cal. yrs BP, possibly caused by a reduction of *Alnus* stands around the lake shore. This may have been a result of the drier climate conditions that had set in at the Atlanticum/Subboreal transition and which are well-documented by lake-level change at Lake Lilla Torkelsjön. As an oligotrophic lake's phytoplankton productivity is often limited by phosphorus rather than nitrogen (Wetzel, 2001, p. 230, 275), this may not be a contradiction. The gradual increase of lake productivity obviously influenced the competition between chironomid taxa sharing the same microhabitat, so that for example, *Micropsectra* was gradually replaced by *Sergentia coracina* in the profundal. The increase of productivity was probably caused by increased erosive processes in the catchment due to anthropogenic disturbance of the surface soils, which is indicated in the massive spread of *Fagus*-forest from 2000 cal. yrs BP on and the concurrent maximum in the abundance of *Sergentia*.

Signs of significant change in pH were not detected in Lake Stora Kroksjön, neither of pre-industrial pH increase or industrial acidification by airborne pollutants. However, Lake Stora Kroksjön has been limed twice to counteract such acidification processes. The fact that the uppermost samples did not reflect such pH changes indicates that

- they either do not represent present-day conditions but were older than assumed, which could have happened through sediment disturbance during the coring and /or extraction process, as well as somewhat erroneous estimation of the exact lake depth at the coring point,
- they integrate a much longer time span in which diatom species indicative of acidified conditions remained rare.

The fact that PCA axis 1 scores of pollen and chironomids show a strong correspondence along the whole sequence (Figure V.17a) suggests that both indicators react to the same environmental forcing. For the late-glacial and much of the Holocene, this would mainly be climate, as this factor influences organisms as well as the surrounding vegetation. In the late Holocene, anthropogenic impact, altering the stability of vegetation cover and top soils, may have overridden the climate signals in both biota via the interactions of vegetation cover of the catchment, erosion into the lake and consequently nutrient input into the lake, affecting the species composition of the water flora and fauna. As the trophic changes mainly affected only two taxa (though these were the most abundant) and PCA integrates the whole chironomid assemblage change, the close correspondence of midge and pollen samples cores allows for the assumption that in the late Holocene, both were primarily, and independently, reacting to climate.

Altogether, Lake Stora Kroksjön has in time of its existence from the early Allerød on been a deep oligo- to mesotrophic lake, just as many others in the region. The main, lasting impact the initial connection to the Baltic Ice Lake had, is the presence of relict crustaceans that may well have exerted structuring effects on the food web of the system, but were not the subject of investiga-

tion in this thesis. The bio-indicators used to reconstruct Lake Stora Kroksjön's paleolimnology show rapid and drastic environmental change at the end of the glacial period, but only small and gradual changes during the Holocene. It also demonstrates how some environmental gradients may cause progressive changes within the species composition of one taxon (e.g., profundal oxygen concentration; *Micropsectra* and *Sergentia*), whereas others in the meantime may act stepwise as thresholds triggering species exclusion, for example nitrate concentration with *Cyclotella 'pseudocomensis'* and *Cyclotella tripartita*.

2 History of Lake Lilla Torkelsjön

2.1 Loss on ignition and core parallelisation

Core parallelisation by matching the LOI curves was somewhat difficult to perform at Lake Lilla Torkelsjön, as the patterns of the sequences showed little difference in absolute LOI values (mean 1.9 %, SD 1.4). Value fluctuations alternated between 240 and 270 cm, suggesting that one of the cores might have experienced some compression in this section (Figure V.3b). However, there were no significant changes in biotic or abiotic characteristics at the levels of transition from one sequence to the next (180 and 285 cm sediment depth, 6000 and 9000 cal. yrs BP respectively). This lead to the conclusion that, though there might be errors within the sequence matching influencing the continuity and age-depth-model of LTO1, these errors are small and do not exceed the amount of one sample stratum (2.5 cm).

2.2 Sediments, core chronology and dating

At Lake Lilla Torkelsjön, the lithostratigraphic boundary between late-glacial and Holocene deposits seems to be well defined by the radical change in lithology. At 340 cm, there was a sharp transition from clayey sands to brown detritus gyttja. Unfortunately, the lower minerogenic part of the core was not dated or analysed further, thus no information about the age of the transition is available. Extrapolation from the last dated level at 310 cm (9503 cal. yrs BP) results in an estimated age of 10,100 cal. yrs BP for the boundary between clastic and organic deposits. As the locality had probably become ice-free around 14,330 cal. yrs BP, according to varve year +20 (Ringberg, 1979), there is a time lag of about 4200 years until lacustrine sedimentation began. Björck and Möller (1987) point out that above the shoreline of the BIL, debris-rich stagnant ice remained in the foreland of the recessing glacier, depositing glaciofluvial sediments during its ablation. The upwards succession of medium-to-silty fine sand implies a dead ice block surrounded by a body of standing water. It is not clear why lacustrine sedimentation lagged as long as it did into the Holocene. On the other hand, undisturbed sediments of the early Holocene seem to be difficult to find in southern Sweden. Preboreal sediments were missing in nearly all Öland lakes studied by Königsson (1968) and several ancient lakes in Skåne had a stratigraphical hiatus (a gap in the chronological succession of sediments) comprising the zones PB and BO1 (Nilsson, 1935). Digerfeldt (1988) presents evidence that these breaks in the sedimentary record may have been caused by a period of extensive aridity during this period, culminating between 9500 and 9200 ^{14}C yrs, that resulted in a lowering of lake level and caused extensive erosion and re-deposition.

It is assumed that Lake Lilla Torkelsjön was affected by this dry period and if any late-glacial lacustrine sediments were deposited prior to this period, they were not reached by the core device through the sandy deposits. The Holocene sediments that consist mainly of algal gyttja of high carbon content, point toward a productive system. The low sedimentation rates indicate that erosion and minerogenic input from the small catchment area was low during most of the Holocene, not diluting any autochthonous organic material deposited. This may be the reason for the higher absolute LOI values compared to Lake Stora Kroksjön. Lake Stora Kroksjön has a much larger catchment in relation to lake surface area and may thus have received more allochthonous material at all times.

2.3 The chironomid record

The first sample analysed for chironomids had a diverse species community with 25 taxa, supporting the assertion that some of the lacustrine sediments are missing at the bottom of the sequence (see Chapter VI.2.2) and the lowermost samples analysed do not represent true pioneering species assemblages. Lake Lilla Torkelsjön supported a chironomid fauna with higher density and species diversity than Lake Stora Kroksjön during the entire Holocene. Among the taxa with a reported depth preference, taxa of the littoral and sublittoral zone such as *Ablabesmyia*, *Dicrotendipes*, *Glyptotendipes*, *Lauterborniella*, *Tribelos*, *Cladotanytarsus*, *Psectrocladius*, *Tanytarsus pallidicornis*, *Corynoneura*, and *Parakiefferiella bathophila* predominate the subfossil assemblage. True profundal species are rare, only *Sergentia coracina*, *Chironomus* spec. and *Tanytarsus lugens* type occur in higher proportions, and taxa typical for deep oligotrophic lakes, like *Micropsectra* and *Heterotrissocladius*, are absent or rare.

The changes the chironomid assemblage of Lake Lilla Torkelsjön has undergone in the course of the Holocene is mostly in the decrease and increase of profundal taxa and a concurrent reversed tendency among the littoral taxa (Figure VI.7). During the Boreal, chironomid zone LTO1-1, *C. anthracinus* and *S. coracina* occurred frequently, but decreased markedly during the period of the Atlanticum and Early Subboreal (zone LTO1-2). During the Subboreal, an increase in littoral taxa, e.g., *Phaenopsectra*, *T. pallidicornis*, *Cladopelma lateralis*, and *Dicrotendipes* is noted. An unknown member of the tribe Chironomini, termed as Chironomini larvula (S. Brooks, pers. communication), also increased markedly during this time and might thus be an unrecognised larval stage of one of the other genera present. Concurrent with the onset of the Subatlanticum (ca. 2600 cal. yrs BP), a re-immigration of the profundal taxa *S. coracina* and *T. lugens* type, suggesting deeper water and/or cooler temperatures, is noted.

During the Holocene, Lake Lilla Torkelsjön seems to have experienced a pronounced water-level lowering, which is supported by regional studies (Digerfeldt, 1988) and the diatom record (see below). Lake Lilla Torkelsjön has always been shallow with a maximum depth of ca. 14.5 m at 10,000 cal. yrs BP (11 water depth + 3.5 m sediment). A lowering of the water level of by two metres would have reduced the lake surface to about the half of its current size (see Figure III.6). Digerfeldt (1988) reports water level changes of a magnitude of up to five metres during the Subboreal in Skåne, a magnitude which would have left Lake Lilla Torkelsjön as a mere puddle or a swamp. Even if the lowering was not so extreme, the chironomids reflect a significant low water period between ca. 5400 to 2600 cal. yrs BP. Factors other than water depth must have

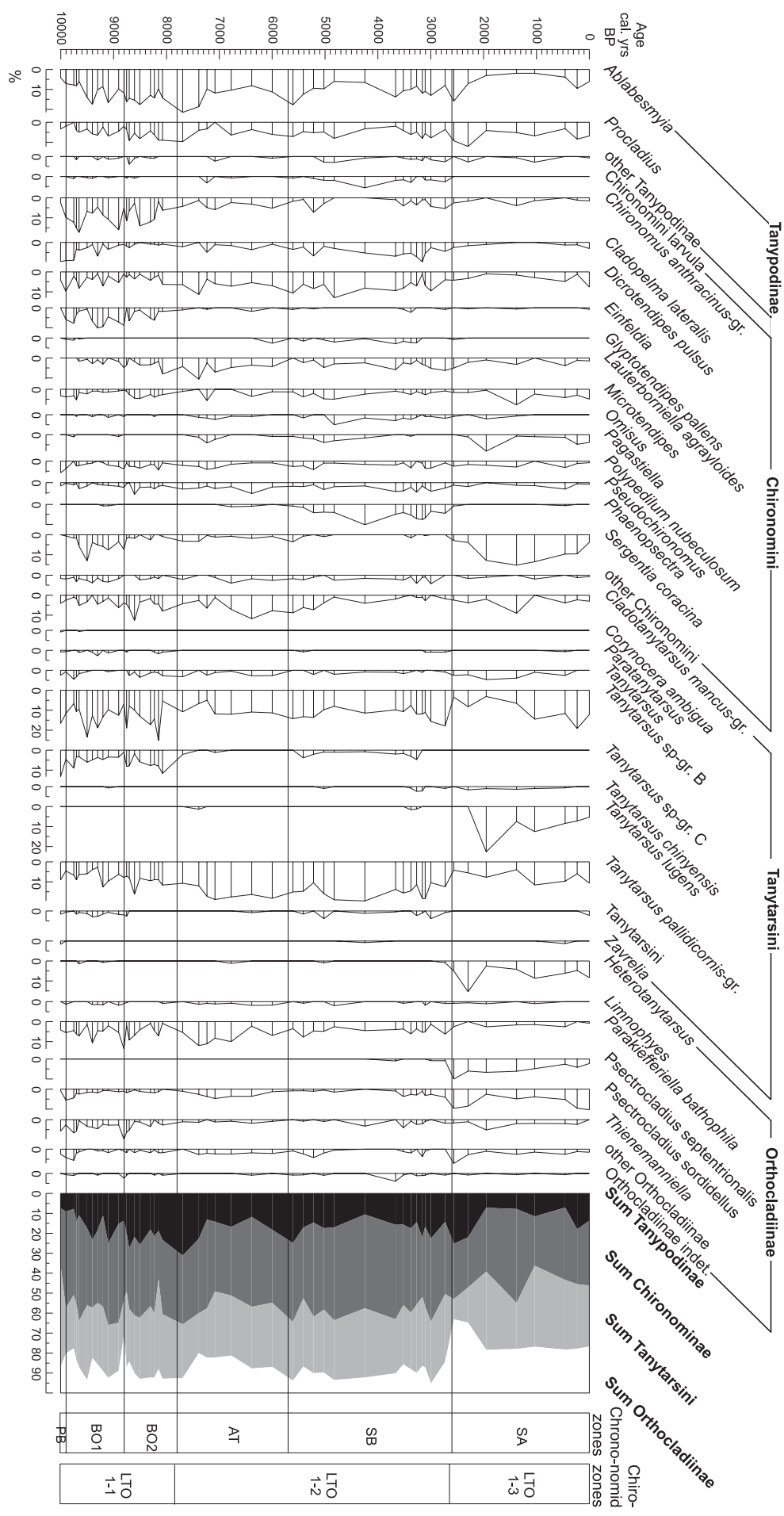


Figure VI.7: Percentage abundance diagram of the chironomids of Lake Lilla Torkelsjön with respect to the Holocene chronozones. Abbreviations: PB = Preboreal, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum

been strongly affected by the change in hydrology, especially water chemistry, but do not seem to have had an impact on the midge fauna composition.

The immigration of chironomid taxa at the SB/SA boundary, coincident with the chironomid zone boundary LTO1-2/LTO1-3 does not only comprise profundal species, but also some taxa commonly related to lower pH, especially *Heterotanytarsus* and *Psectrocladius* spec.. The diatom assemblage gives evidence of just the contrary (see Chapter VI.2.4). As diatoms are known to be greatly sensitive towards pH and may thus possibly provide more accurate picture of past pH conditions, the chironomid signal may be interpreted in terms of habitat structure, as *Heterotanytarsus* and *Psectrocladius* spec. are also macrophyte-dwellers. Species expansions may thus have been related to the development of submerged macrophytes. These are likely to have extended significantly with the late-Holocene lake-level rise, given the fact that a huge part of the lake area has a water depth of less than two metres.

The decrease of Tanypodinae, especially *Ablabesmyia*, in the Subatlanticum might perhaps be connected to the presence of *Chaoborus flavicans* in distinctly higher densities (see Figure V.11). Both predatory larvae may be competing directly for food, or be subject to predation themselves, even though *Chaoborus* forages nocturnally in the pelagial (Sæther, 1972).

The trophic development of Lake Lilla Torkelsjön is difficult to assess by interpreting the fossil chironomid assemblage. The absence of a true profundal zone and thus the absence of taxa sensitive towards oxygen depletion gives no information about possible eutrophication processes. The presence of such taxa as *Glyptotendipes* and *Chironomus plumosus* that thrive best under high nutrient conditions (Sæther, 1979) suggest that productivity was at least moderate during the Subboreal. However, the Subatlantic maximum of *Sergentia coracina*, occurring concurrently with the *Fagus*-maximum, is a feature Lake Lilla Torkelsjön has in common with Lake Stora Kroksjön and which, knowing that *Fagus*-seeds are competitive in disturbed topsoils, can be interpreted as an increased erosive input into Lake Lilla Torkelsjön in this period, likely enhancing the productivity of the system.

The chironomid assemblage of Lake Lilla Torkelsjön appears temporarily influenced by factors indirectly related to temperature and consequently, climate. Significantly high rates of change are attained at the Preboreal/Boreal boundary and at the early/late Boreal boundary (Figure V.12b), the first of which rather suggests a direct linkage between the midge fauna development and climate. The BO1/BO2 boundary, however, seems in Blekinge to be related to forest succession (the replacement of *Pinus* by *Corylus, Quercus, Ulmus, Tilia*, Chapter VI.1.5) and may have had effect on the trophic situation at Lake Lilla Torkelsjön. Seppä and Weckström (1999) state that soils under conifer stands are much richer in DOC and TOC. The forest succession towards deciduous trees may have decreased the nutrient transport into Lake Lilla Torkelsjön such that primary production may have decreased, subsequently leading to lower food availability for the midge assemblage.

2.4 The diatom record

The diatom flora of Lake Lilla Torkelsjön has undergone two significant changes in composition during the Holocene, which seem to be forced by lake hydrology and pH. Some *Fragilaria*-species were found only in the early Holocene and were possibly remnants of the

pioneer assemblage (see Figure VI.8). Benthic diatoms were present, but the assemblage was dominated by the planktonic centroids *Cyclotella stelligeroides* and *C. stelligera*, suggesting a deep, oligotrophic lake.

Around 4400 cal. yrs BP, at the early/late Subboreal boundary, the disappearance of planktonic species indicates a radical change in lake hydrology. The water volume of Lake Lilla Torkelsjön was reduced to such an extent that a suitable pelagic habitat for planktonic diatoms was non-existent. Planktonic diatoms are dependent on turbulent mixing in the water column in order to reproduce. The morphology of Lake Lilla Torkelsjön makes it likely that even a moderate water level lowering of ca. two metres (values of up to five metres water level reduction are documented from adjacent regions for the period in question (Digerfeldt, 1988); changes of groundwater levels of up to 1.5 meters are registered regularly in Blekinge as documented by Pousette et al., 1983) would have resulted in reduced water mixing. About half of the lake basin is shallower than two metres, only a small area close to the southern shore is deeper and would have remained flooded, resulting in a small wind fetch (see Figure III.6). The wooded hills surrounding the lake further protect the water surface from wind. Thus, even if the water column in the central basin was several meters deep, it was not necessarily suitable to host pelagic diatom species.

Concurrent with the disappearance of pelagic diatoms, a drop in lake water pH is indicated by the increase of acidophilic diatom species such as *Brachysira brebissonii* and *B. styriaca*, *Fragilaria gracilis*, *Frustulia crassinerva*, and *F. saxonica*. It seems plausible that the drop in lake water pH is linked with the change in hydrology. If the water level was reduced to a magnitude of two metres, nearly half of the former lake bottom would have fallen dry. Enhanced nitrification processes of the exposed organic material can have produced acid compounds that subsequently leached into the lake basin. The pH may have changed up to 1 pH unit, possibly from around 6.5 to close to 5.5 (P. Hamilton, pers. comm.).

From ca. 2600 cal. yrs BP (zone LTOdia-4), planktonic species (mainly *Aulacoseira* spec. and *Cyclotella* spec.) immigrate into the lake, indicating a rise of water level. Concurrent with basin infilling, signs of increasing pH can be detected. The change in water level may have played a role, but more likely, the increase of human activity in the catchment was responsible. A diatom-inferred pH increase between 2300 and 1000 ^{14}C BP has been registered at numerous sites over southern Sweden (Renberg et al., 1993). They suggest that following the expansion of the agrarian economy during the Iron Age, forest burning, grazing and agriculture increased the base saturation and pH of the soils, thus enhancing the transport of base cations and nutrients into the surface waters. This phenomenon has been recorded in a variety of sites over southern Sweden, and its asynchronity suggests sources other than climatic forcing. At Lake Lilla Torkelsjön, the effect is visible as a decrease in the acidophilic species such as *Brachysira brebissonii*, *B. styriaca*, *Fragilaria gracilis*, *Frustulia crassinerva*, and *F. saxonica* and the increase of the alcalophilic *Fragilaria exigua* after 2600 cal. yrs BP. Hence, increase of pH at this time is interpreted as an indication of human activity in the lake catchment. The uppermost sample does not reflect the recent acidification caused by airborne pollution, which has affected many Swedish lakes on acid bedrock (Almer, 1974; Renberg et al., 1993). The disturbance of sediment layers at the sediment-water interface by coring and the low temporal resolution, which is too low to discern effects occurring on a decennium scale, may be reasons for this.

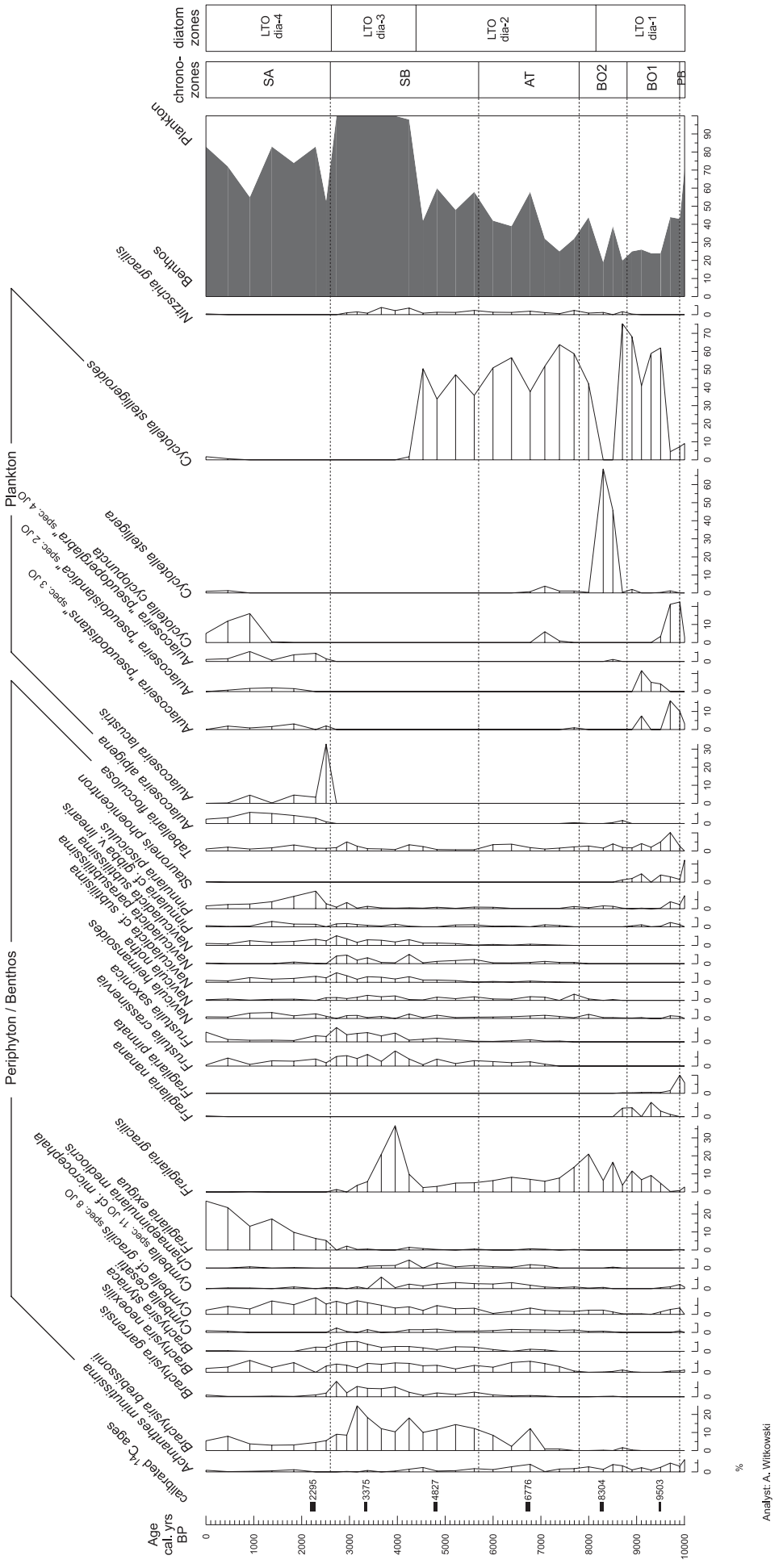


Figure VI.8: Percentage abundance diagram of selected diatoms of Lake Lilla Torkeljön with respect to the late-glacial and Holocene chronozones. Abbreviations: PB = Preboreal, PBO = Preboreal Oscillation, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum. JO: Julma Ölkky, species sensu Lange-Bertalot and Metzelin (1996).

It is remarkable that the drastic changes in lake hydrology are not reflected in the pattern of species diversity development (Figure V.22). The increasing trend remains unbroken, even through the period when the planktonic flora was absent from the assemblage. There are no signals for eutrophication processes among the diatoms of Lake Lilla Torkelsjön, but the assemblage remains typical for oligo- to mesotrophic conditions throughout the whole sequence.

2.5 Vegetation history

The pollen diagram of Lake Lilla Torkelsjön is similar to that of Lake Stora Kroksjön in respect to major tree, shrub and herb species. The lowermost sample is likely from the boundary of the Preboreal/Boreal chronozone (ca. 9900 cal. yrs BP) and captures the beginning expansion of the mixed broad-leaved forest of *Quercus*, *Ulmus*, *Alnus* and *Tilia*. This forest type and *Quercus* in particular, reached higher percentages than at Lake Stora Kroksjön, whereas pine pollen were of lower abundance (Figure VI.5). This difference is probably not due to locally differing forest vegetation, but to the different lake surface area. Long-range distributed pollen (e.g., *Pinus*) is very dependent on the lake size (Lindbladh et al., 2000), with small lakes capturing considerably less long-distance transported pollen than larger ones. The lower percentage of *Pinus* in turn leads to higher percentages of other pollen types. The other main difference relative to Lake Stora Kroksjön was a higher percentage of birch pollen during the Subatlanticum, which indicates a more open landscape in the pollen source area of this site. The indicators for meadows (Poaceae < 40 μm and *Plantago lanceolata*) and pasture (*Juniperus* and *Calluna*), first becoming abundant at the onset of the Subboreal (ca. 5700 cal. yrs BP), were overall somewhat higher here than at Lake Stora Kroksjön, probably because Lake Lilla Torkelsjön lies closer to the open Mieån River valley, along which an exploitation of the inland areas may have taken place.

Picea abies was present locally for the past 400 years, and its abundance appears to be increasing. Human plantation and soil disturbance have favoured its southward migration (Björkman and Bradshaw, 1996). Today, Lake Lilla Torkelsjön lies on the very southern limit of its distribution, as can be deduced from its near-total absence at the site of Lake Stora Kroksjön, only 5 km further south.

The asynchronities in pollen zone boundaries between Lakes Stora Kroksjön and Lilla Torkelsjön are probably not a result of an asynchronous climate-driven vegetation development at the two sites, but more likely local differences in vegetation communities and/or coarse subsampling. Additionally, climate effects that result in more or less equal vegetation patterns on a regional scale are overridden by human activity in the pollen source area beginning from the end of the Atlanticum.

2.6 Other proxies

Loss on ignition

The sedimentation of organic material at Lake Lilla Torkelsjön has undergone some distinct changes within the Late Holocene. An increase in LOI is especially obvious in the Late Subboreal (Figure VI.9), while a increasing tendency can already be noted at the end of the Atlanticum. Loss on ignition is the product of both autochthonous and allochthonous processes (see Chapter VI.1.1). High LOI values may be due to a high lake productivity as well as low minerogenic in-

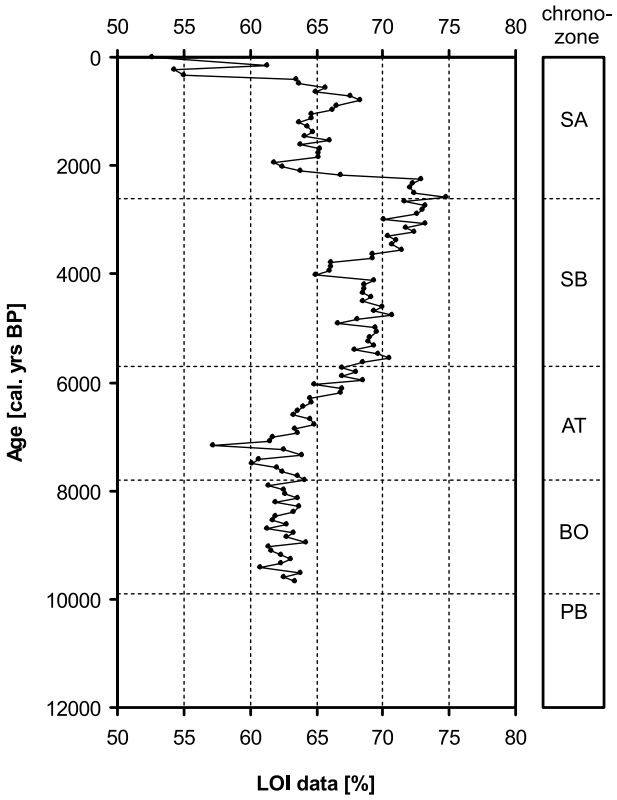


Figure VI.9: Loss on ignition data at Lake Lilla Torkelsjön. Abbreviations: PB = Preboreal, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum.

put from the basin catchment. In the case of Lake Lilla Torkelsjön, a significant increase of lake productivity at this time can not be deduced from the chironomid or diatom community reactions, whereas there is clear evidence for low water levels in the diatom record (Chapter VI.2.4). As decreasing groundwater and lake water levels have in southern Sweden been linked to periods of low precipitation (Digerfeldt, 1988), the increase of LOI at Lake Lilla Torkelsjön is interpreted as a signal of dry climate during the Subboreal. Subsequently, a LOI decrease at 2600 cal. yrs BP happens contemporaneous with the re-establishment of a pelagic diatom flora and the immigration of deep-water chironomids, such as *Sergentia coracina* and *Tanytarsus lugens* type. This suggests a rise in water level and thus, an increase in precipitation. The autochthonous organic sedimentation may have been diluted by minerogenic input from the catchment. Additionally, increased human activity in the catchment may have contributed to enhanced soil erosion, as suggested for southern Sweden by Renberg et al. (1993), starting around 2500 cal. yrs BP, corresponding roughly with the results at Lake Lilla Torkelsjön. Thus, LOI gives additional evidence for changes from wetter to drier climate at the early/ late Subboreal boundary (ca. 4000 cal. yrs BP) and drier to wetter conditions around 2600 cal. yrs BP. Evidence for a dry period between ca. 4900 and 2600 ^{14}C yrs has also been brought forward by Digerfeldt (1988) and earlier by Berglund (1966b).

Chaoborus mandibles

The mandibles of the dipteran *Chaoborus flavicans* have only been found in higher amounts in the upper part of the Lake Lilla Torkelsjön sequence (Figure V.11). The predatory midge can tolerate severe oxygen depletion and is often found in lakes with hypolimnetic anoxia and hypertrophic lakes (Löffler, 1986; Hofmann, 1971a). The fact that *C. flavicans* became abundant after Lake Lilla Torkelsjön became deeper suggests that the lake experienced lowered oxygen concentrations in the deepest part at this time, even though organic deposition is lower. Human activity in the vicinity, also detected by the pollen record and likely the diatom assemblage, may have led to higher nutrient loading of the lake water and consequently to oxygen depletion in the deepest part of the lake. The morphology of Lake Lilla Torkelsjön with a small pit-like deep part (see Figure III.6) may have additionally prevented water circulation and distribution of oxygen in the whole of the water column.

2.7 Climate reconstruction

At Lake Lilla Torkelsjön, inferred Holocene July temperatures ranged from 10.7 to 15.3 °C and were thus almost consistently higher than those inferred at Lake Stora Kroksjön. The sample-specific prediction errors have the same magnitude as at Lake Stora Kroksjön, with a mean of ±1.10 °C. The modern analogue situation at Lake Lilla Torkelsjön is generally good, as all samples had analogues among the modern data set, and most of the samples are even classified as having good analogues (see Chapter V.3.5), despite the fact that the taxon *Einfeldia*, which is not present in the Norwegian calibration set, did reach abundances of up to 10 % in early Holocene samples.

The general temperature trend is consistent with other climate reconstructions during the early and mid-Holocene period, but deviates during the Subboreal chronozone. In the following, the temperature reconstruction will be assessed in further detail.

From the beginning of the Boreal, the general warming trend is punctuated by several drops in temperature with an amplitude of about 1 °C (at 300, 270, and 245 cm, dated 9300, 8700, and 8150 cal. yrs BP, respectively). The significance of these deviations from the general trend is difficult to assess, as they all are well within the prediction error of the inference model. However, the drop around 9300 cal. yrs BP is in good temporal agreement with one of the ice-rafting events described by Bond et al. (1997), AMS-dated to 9400 cal. yrs BP (event number VI, Figure VI.6) and further supported by a concurrent minor drop in the LOI curve at 9400 cal. yrs BP (see Figure V.11). On the other hand, the temperature drop at 8700 cal. yrs BP has no such representation in other climate archives or the lake productivity curve and may thus probably be noise. Bond's event number V (8100 cal. yrs BP), the 8.2 event, again is well-represented in the inferred temperatures of both in Lakes Lilla Torkelsjön and Stora Kroksjön. The 8.2 ka event (e.g., Alley et al., 1997; von Grafenstein et al., 1998) at Lake Lilla Torkelsjön had an amplitude of 0.8 °C and a possible maximum duration of 150 years. Timing and amplitude correspond well with other reconstructions.

In the course of the Atlanticum, inferred temperatures reach a maximum between 7300–7000 cal. yrs BP with around 14.5 °C, then decrease towards 13 °C between 6700 and 5200 cal. yrs BP. During the Subboreal, inferred temperatures rise to values above 14 °C for a period of nearly 2500 years. This pattern deviates substantially from the

general climate patterns and is most likely linked with the low water levels at Lake Lilla Torkelsjön during this period. During this time, the samples have poorer analogues among the modern data, incorporating several warm-water taxa, e.g., *Glyptotendipes* and *Omisus*, that occurred rarely and in low frequencies at sites with warm summer temperatures in the training set.

Trends and patterns of the temperature reconstruction show strong similarities between Lakes Lilla Torkelsjön and Stora Kroksjön until the end of the Atlanticum, suggesting that the midge assemblages responded to the same environmental forcing during this period. During the Subboreal, however, local conditions at Lake Lilla Torkelsjön override the regional signal and lead to a different midge response. The low water level, indicated by diatoms, is assumed to be the driving factor in inferring high temperatures. High summer insolation may cause water temperature of a shallow lake to rise significantly above air temperature, let alone monthly means (Walker et al., 1997). This fact may compromise chironomid-based temperature reconstructions in very shallow water bodies, as it allows for warm-stenothermic chironomid taxa to successfully compete in a habitat that would otherwise under the same climate conditions provide temperatures below the species' optimum. Thus, considering general regional climate trends derived from other reconstructions, as well as indication from Lake Stora Kroksjön that local microclimate probably was not deviating from the general trends, it has to be assumed that the temperatures inferred during the Subboreal do not reflect the local climate adequately. However, the similar development of chironomid and pollen sample scores (Figure V.17b) suggests that the midge community responded to the same environmental forcing as the vegetation in the vicinity of the lake, which is most probably climate.

The diatom record, showing acidification but not eutrophication trends for the low-water period, makes it possible to eliminate trophic changes affecting chironomid-based temperature reconstructions as climate warming. Brodersen and Anderson (2002) suggest that it may be difficult to separate the influence of productivity from the influence of temperature on chironomids, as nutrient increase as well as warm water conditions favour the immigration of a eutrophic-indicating chironomid assemblage with high temperature optima. The signal may, in both cases, be a rise in inferred temperatures.

The coolest temperatures of the Holocene are inferred from the Subatlanticum. The cooling trend, beginning ca. 2600 cal. yrs BP, leads to mean temperatures below 12 °C. For 1950 cal. yrs BP, the minimum value of 10.6 °C was inferred. Matthews et al. (2000) present evidence for minor glacier advances in southern Norway between 2200 and 1800 cal. yrs BP, terming it the Bøvertun I event. Signs of the 'Little Ice Age' are not clearly discernible from the general temperature fluctuations, though the sample dated 460 cal. yrs BP (AD 1490) infers slightly cooler values than the samples before and after. Dating uncertainties may play a greater role in the samples between sediment surface and the first dated horizon, as the age of the surface sample is modelled as zero (AD 1950), but may be older due to disturbance during coring and core extrusion.

In the course of the Holocene, there are several climate reversals that cannot easily be linked with to those presented by Bond et al. (1997), though some of them are consistently represented in both Lakes Lilla Torkelsjön and Stora Kroksjön (e.g., 6350, 3130 cal. yrs BP). These may tentatively be related to Bond events IV and II (Figure VI.6), though their significance could only

be assessed by a higher sampling resolution and an improved chronology. Moreover, not all events described by Bond et al. (1997) are detected in the temperature reconstruction at Lakes Lilla Torkelsjön or Stora Kroksjön. Dating uncertainties and coarse sampling resolution may be responsible as well as complex linkage of the local microclimate to the ocean circulation changes in the North Atlantic.

Altogether, trends and states of the chironomid-inferred temperature reconstruction at Lake Lilla Torkelsjön seem to produce reliable data during the Holocene, with the exception of the Subboreal period, when inferred values are probably too high.

2.8 LTO Synthesis

All indicators analysed from Lake Lilla Torkelsjön show that the lake has undergone severe changes within the last 10,000 years in terms of hydrology and, to a lesser extent, trophic status. The environmental conditions under which limnic sediments were first deposited remain unclear, but it seems that a hiatus exists between the clayey sands below 340 cm and the gyttja sediments above. This may have been caused by dry climate conditions in the Preboreal (Digerfeldt, 1988). From 340 cm, Lake Lilla Torkelsjön shows features of an oligotrophic lake, in terms of the diatom flora. The first sample (10,003 cal. yrs BP) includes numerous benthic diatom taxa, reflecting the long ice-cover under the Preboreal climate conditions and thus confirming the age-depth-model that extrapolates a Preboreal age for the sample.

During the Boreal, chironomids typically dwelling in sublittoral and profundal zones were present, indicating that water depth was sufficiently high to accommodate their habitat requirements. These species became less abundant or even disappeared during the Atlanticum and Subboreal, whereas typical littoral inhabitants immigrated into the system or, when they had been present before, increased in their abundance (Figure VI.10). Low water levels, as indicated by chironomids, were registered during the period from ca. 4900 until 2600 cal. yrs BP. The diatom record with the dominance shift from planktonic to benthic ecotypes and back again indicates low water levels between 4400 and 2600 cal. yrs BP. LOI suggests a period of lowered erosive input of clastic material from ca. 4700 cal. yrs BP to 2600 cal. yrs BP with a short break from 4100 until 3800 cal. yrs BP and a maximum from 3800 until 2600 cal. yrs BP.

The synthesis of the indicators suggest that the lake water level was already considerably lowered in the early Subboreal (around 4900 cal. yrs BP) so much so that a true profundal zone was no longer present at Lake Lilla Torkelsjön. The lowering continued, probably because of continuing low precipitation and/or high evaporation, until around 4400 cal. yrs BP, when the water level fell below a critical value which led to the exclusion of planktonic diatoms from the species assemblage. The low water levels likely prevailed until between 2600 and 2250 cal. yrs BP, when pelagic diatoms and sublittoral chironomids were present again and the proportion of clastic material increased.

Lake-level fluctuations, as they are reconstructed for Lake Lilla Torkelsjön, may be the result of regional climate change, and also stem from local environmental changes e.g., lowering of the outflow threshold by erosion, damming of the outflow by peat growth, or human activity such as damming or artificial lowering. However, more-or-less synchronous lake-level changes are reported from a large area in southern Swe-

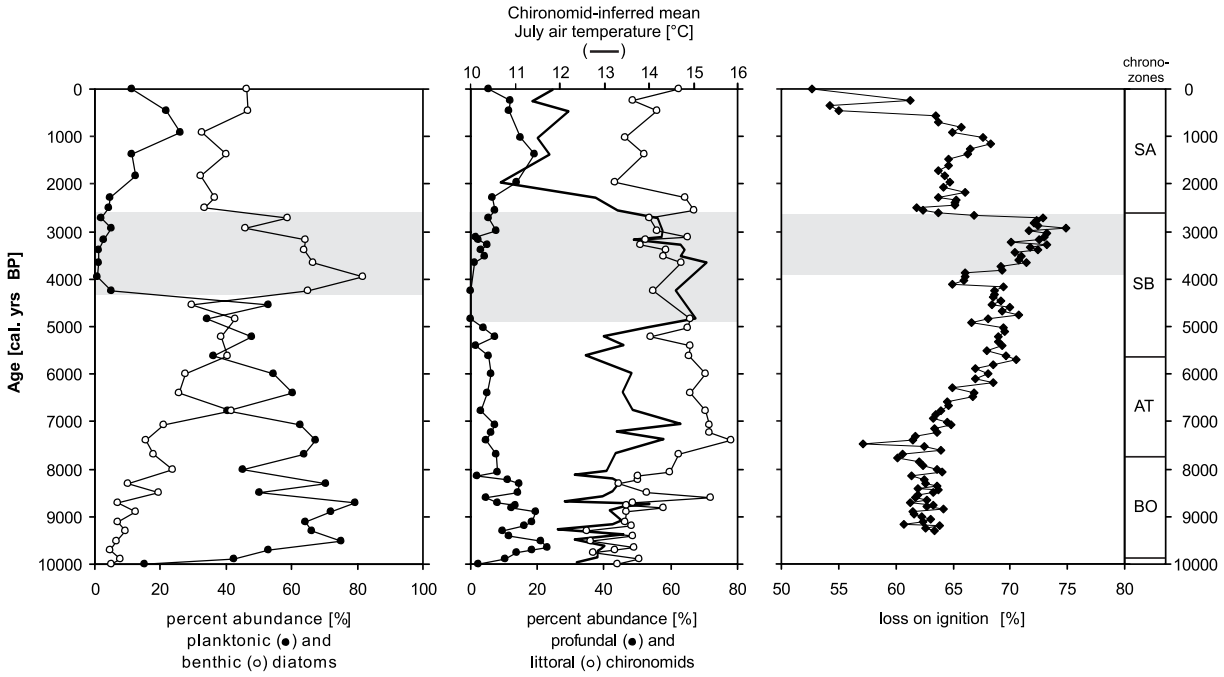


Figure VI.10: Diatom forms, chironomids and temperature reconstruction, and loss on ignition at Lake Lilla Torkelsjön. Shaded areas: Indication for low water levels (diatoms), warm climate and low water levels (chironomids), and low precipitation (loss on ignition). Abbreviations: BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum

den and suggest climate-induced hydrological changes (Digerfeldt, 1988; Gaillard and Digerfeldt, 1991). Thus, periods of low groundwater and lake levels are attributed to decreased average humidity. The period of decreased water levels at Lake Lilla Torkelsjön seems somewhat late compared with other sites presented by Gaillard and Digerfeldt (1991), where the second major period of lowered water levels in the Holocene starts in the late Atlanticum and is centered around the early Subboreal (5600 to 3900 cal. yrs BP). However, chironomids at Lake Lilla Torkelsjön indicate low water levels already as early as 4900 cal. yrs BP. The late low water signal of the diatoms may be due to the fact that the water level values fell below a critical ecological threshold much later than initial lowering, emphasising the long-term trend of the hydrological process. The increase of water levels appears to have started already by 3100 cal. yrs BP, but until 1800 cal. yrs BP, planktonic diatoms made only up a small part of the species assemblage.

The infilling of the basin, happening synchronously with rising lake levels at various sites in southern Sweden, is a result of the cooler and wetter climate of the Subatlanticum and not of artificial damming. However, the decrease of acidophilic diatom taxa, indicating rising pH, suggests human activity in the lake catchment. Forest burning and grazing, indicated somewhat later by the increase of *Fagus*-pollen, took effect by enhancing the transport of base cations and nutrients into the surface waters, triggering eutrophication processes. A change in trophic status is further indicated by the increased presence of the phantom midge *Chaoborus flavicans*. Phantom midges are tolerant to oxygen depletion and even anoxia. However, the presence

of oxygen-demanding profundal chironomid taxa indicates that oxygen depletion in the hypolimnion can only have been moderate. Hence, lake productivity, though probably higher than in the early Holocene, was moderate even in the late Holocene. Today, Lake Lilla Torkelsjön is considered mesotrophic.

The chironomid-inferred temperature reconstruction shows a pattern that deviates from the well-established Holocene temperature trends reconstructed from ice cores (Dahl-Jensen et al., 1998), glacier margin movements (Nesje and Kvamme, 1991), and pollen (Seppä and Birks, 2002). Maximum temperatures were inferred from the Subboreal instead of the early Holocene. The rise in temperatures coincides with the first signs of lake-level lowering, when profundal chironomids disappear from the assemblage, indicating that the lake did not provide a sufficiently cool habitat for these taxa between 4900 and 2500 cal. yrs BP. Most of the remaining littoral taxa have high modelled temperature optima within the Norwegian calibration set (see Figure IV.2). It is assumed that the air temperatures inferred from these samples are probably too high. In this section, air and water temperature may not have had the same correlation as when Lake Lilla Torkelsön had a larger water volume and the reconstruction seems to be compromised by the fact that chironomids are more directly influenced by water temperature than air temperature. The basic assumption underlying the climate inference model used is that the relationship of air and water temperature is mainly linear. However, it has to be acknowledged that this relationship may not be straight-forward in all places and at all times, as it incorporates many factors as e.g., lake depth, temperature of inflowing water, evaporation from lake surfaces, and loss of radiation by reflection off the water surface (Walker et al., 1997). At Lake Lilla Torkelsjön, the small water volume during the Subboreal probably led to a higher summer warming than when the lake was deeper, allowing chironomids with a high thermal optimum, especially *Omisus*, to colonise despite generally cooler air temperatures than in the Atlanticum.

Lacking sufficient taxonomic overlap with the available diatom-inferred pH transfer functions of the region, the pH reconstruction performed with the SWAP data set did not provide reliable data. However, it did support the notions of the qualitative evaluation that pH was lower during the period of low water levels. The lower water level is thought to have led to natural acidification probably through nitrification processes of the organic material exposed to oxygen. This development was reversed when water level rose. Rising pH and eutrophication was then probably enhanced by human influence. However, recent acidification trends could not be detected in the uppermost sample, likely because it integrated a period longer than airborne acidification has acted upon Scandinavian waters.

Mantel's test revealed significant correspondence between changes in the diatom and chironomid assemblage. This is not unexpected, seeing that the hydrological changes at Lake Lilla Torkelsjön affect both biota's species composition, especially in terms of depth requirements. The fact that PCA axis 1 scores of pollen and chironomids show strong correspondence (Figure V.17b) leads to the same conclusions as at Lake Stora Kroksjön. It is assumed that both groups show the same trends in sample scores because they both respond to climate. Vegetation lags somewhat behind the chironomid development, which is in good agreement with the ecological assumption that midges should respond more promptly to environmental change than vegetation due to their comparatively short life cycle. The correspondence between the three biota, though evaluated by different multivariate

approaches, shows that the changes at Lake Lilla Torkelsjön were ultimately controlled by climate, as for example, changing water levels (and thus changing pH) were a result of changing net humidity as a function of precipitation and temperature.

3 Regional synthesis

Following the extensive investigations of Berglund (1966a; 1966b) on late-glacial and Holocene vegetation development, a number of paleoenvironmental investigations comprising sedimentological, stable-isotope, paleomagnetic, palynological, macrofossil, and diatoms have dealt with the paleoenvironmental history of southern Sweden and Blekinge since deglaciation. The main focus has been put on the pattern of shoreline displacement of the Baltic Sea (e.g., Björck, 1979; Liljegren, 1982; Yu, 2003), on the paleoecology of the Late Weichselian/Holocene boundary (e.g., Ising, 2001), and Holocene changes in hydrology (e.g., Digerfeldt, 1972; 1988; Hammarlund et al., 2003). This thesis presents a multi-proxy approach focusing on the biological records and integrates quantitative paleoclimatic reconstructions from two sites lying in close vicinity of each other covering the whole of the Holocene.

Freshwater lakes, and especially lakes from the northern temperate regions, are ecosystems that have been studied extensively in the history of limnology. Therefore, the ecological mechanisms and interactions of abiotic and biotic compounds of lakes and their catchment are comparatively well understood (Wetzel, 2001). This may make it possible to relate biotic change observed in the sediment record to the environmental variables governing this change. In this case, the two within-lake biota (midges and diatoms), the vegetation of the catchment and the organic sedimentation of the two sites investigated form the basis on which the regional environmental reconstruction is grounded. In the following, a comparison of the sites will be done in the light of the zonation results and the variables identified as having influenced the individual development of the sites.

3.1 Zonation

Organisms may respond to different environmental variables at different times. In each lake with its own abiotic circumstances, with its unique combination of taxa, each of which has its own environmental optimum and tolerance, significant compositional turnovers may happen at a different time during periods of gradual environmental change. Based on this assumption, it is thought that only when there is a sudden and high amplitude environmental change, like the temperature changes that occurred on several occasions during the late-glacial, a synchronous signal may be expected (Brooks, 2000). This effect is not observed in the results of this study (Figure VI.11), as significant species turnovers at Lake Stora Kroksjön occur exclusively during the Holocene. The between-site and between-biota comparison (Figure VI.11) indicates that three periods of high-amplitude environmental change emerge: the end of the Preboreal, the onset of the Atlanticum and the onset of the Subatlanticum. The fact that several zone boundaries are more or less concurrent with these chronozone boundaries leads to the conclusion that even though the lake biota responded probably to a combination of environmental variables during the Holocene, climate likely had, directly or indirectly, an ultimate control on most of these variables. Additionally, it becomes clear that in periods of gradual

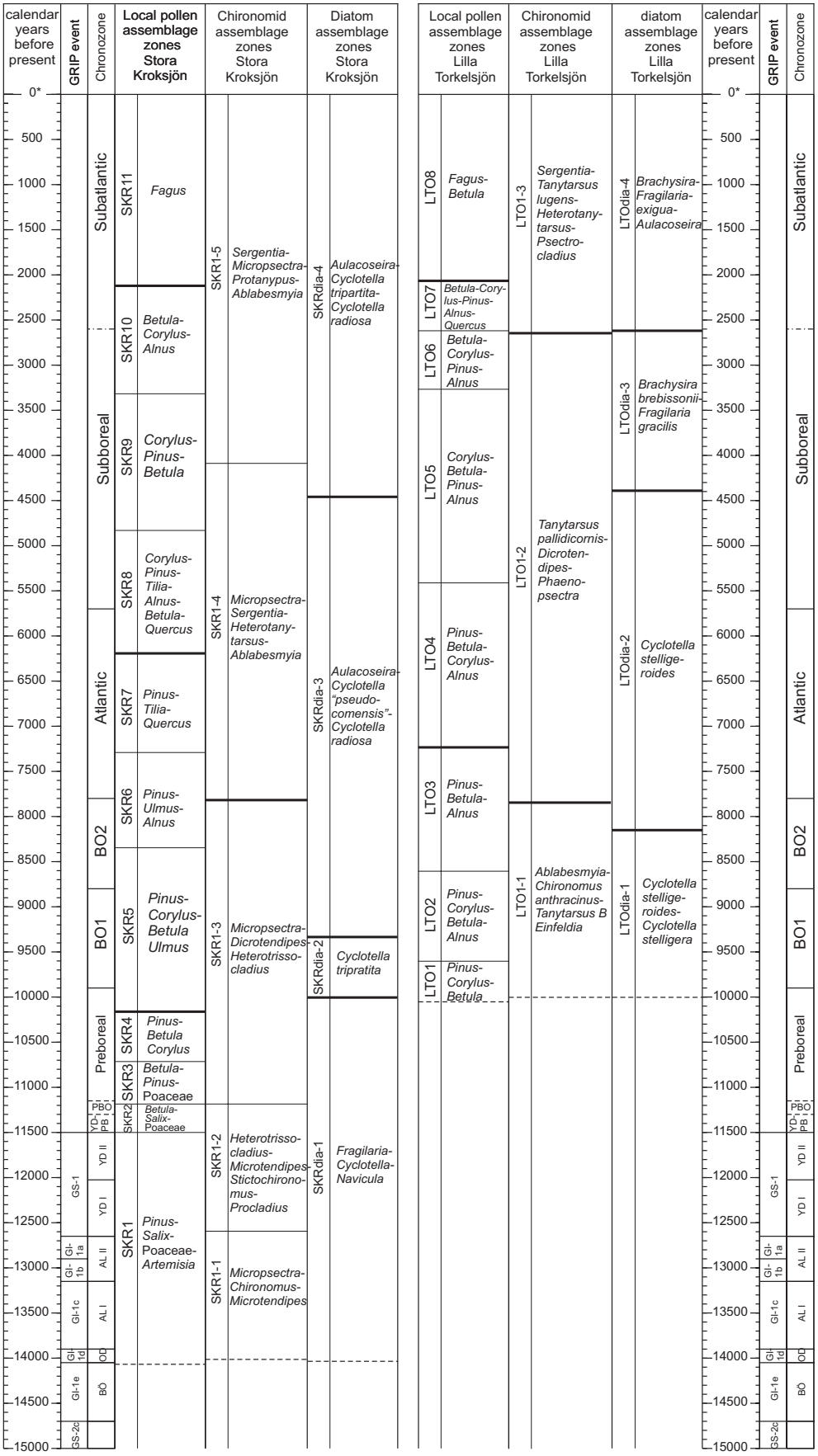


Figure VI.11: Changes in the chironomid, diatom and pollen records. Fat lines mark significant zone boundaries assessed by sum-of-squares optimal partitioning criteria tested on a broken-stick model. Dashed lines indicate the base of the respective analysis. Abbreviations: AL = Allerød, YD = Younger Dryas, PB = Preboreal, BO = Boreal, AT = Atlanticum, SB = Subboreal, SA = Subatlanticum; GI, GS = Greenland Ice core record stadial and interstadial events. Dash-dotted line at the SB-SA boundary: Boundary still in discussion.

climate changes, as during the Holocene, such change may cause significant concurrent turnover of biota on a regional scale. Looking at concurrent biotic responses, the changes at the end of the Preboreal and the onset of the Atlanticum are most likely results of the forest succession and thus, albeit only indirectly, linked with climate. Changes in forest composition had an impact on soil stability and development, on the amount and chemical composition of runoff and groundwater transported into the lakes, ultimately influencing the nutrient availability in the lakes. The concurrent zone boundaries at the Subboreal/Subatlantic transition however are partly related to anthropogenic impact (vegetation) and lake hydrology change (biota of Lake Lilla Torkelsjön) and thus only partly to climate.

3.2 Climate

The signals of regional climate change are reflected in the biota of both lakes, though, due to the different lake types, with varying intensity. In spite of the fact that temperature was not the main gradient during all of the Holocene, but climate was on a broader scale acting upon the lake biota, the Holocene temperature trends generally showed good agreement at both sites, with the exception of the Subboreal chronozone when the differing lake depth had an effect on the absolute temperature outcome. Late-glacial and early Holocene temperatures were generally low, rising to a mid-Holocene maximum at both sites. Cold oscillations, like the 8.2 event, are equally documented by the vegetation and the midge fauna at both sites. During the Subboreal however, the regional signal was clearly overridden by the local circumstances in Lake Lilla Torkelsjön. The coldest Holocene temperatures were inferred for the Subatlanticum, which corresponds with general evidence for cooler climate in the last 2000 years.

Apart from temperature, other climate signals are reflected, as well. Dry periods during the Preboreal and Subboreal are reflected in Lake Lilla Torkelsjön by a sediment hiatus and the response of diatoms and midges, demonstrating the sensitivity of shallow lakes towards water-level fluctuations. There is no response of the biota within the lake to dry periods at Lake Stora Kroksjön, but the pollen record hints towards changes in the surrounding vegetation. Signs of decreased erosion during the Subboreal are present at both lakes; LOI values are highest in the same period, indicating decreased precipitation.

3.3 Productivity changes

It may be difficult to distinguish between changes in temperature and productivity, as an increase in nutrient load often is accompanied by an immigration of eutrophic-indicating chironomid fauna with high temperature optima (Brodersen and Anderson, 2002). The oligotrophic cold-water fauna of deep stratified lakes, on the other hand, may remain unperturbed by temperature increases due to their thermic isolation. If, however, increased productivity leads to increased oxygen consumption in the hypolimnion, the profundal chironomid assemblage will be affected. The changes in the profundal midge assemblage of Lake Stora Kroksjön from the Subboreal on were probably triggered by increased nutrient input and moderate oxygen depletion. Concurrent with the signs of gradual eutrophication, the vegetation indicated increasing human agricultural activity in the area. With *Sergentia* attaining highest percentages in the time when beech-forest becomes established, a link between lake productivity and erosive input into the lake seems to be established. *Fagus*-seeds are highly competitive in dis-

turbed topsoils, and its spread was probably favoured by forest grazing of domestic animals such as pigs, which turn up the upper soil layers in their search for seeds and roots. However, natural productivity increases may also be triggered by changes in the forest composition in a lake's catchment. Soil solutions under conifer stands are much richer in TOC and DOC than those under deciduous trees (Seppä and Weckström, 1999) and may lead to eutrophication and acidification. But as no sign of forest compositional change was noticed, and *Pinus* decreased in abundance during the Subboreal and early Subatlanticum, it is thus concluded that the increase in nutrient load of surface run-off into Lake Stora Kroksjön was likely caused by human disturbance of the top soils, animals and forest burning. At Lake Lilla Torkelsjön, the aforementioned effect of eutrophication on the chironomid-inferred temperatures could be suspected during the Subboreal, but there are no such signals from the diatom flora, which are typical for oligotrophic conditions. A similar increase of *Sergentia*, concurrent with the spread and decrease of beech forest, can be noted as well as abundant mandibles of the phantom midge *Chaoborus flavicans*, indicating a productivity increase at Lake Lilla Torkelsjön after 2000 cal. yrs BP. This effect, where eutrophication and warm inferred temperatures are indicated in the midge fauna is not present at either of the sites, as in the periods with highest trophic conditions (which still by no means can be called eutrophic) produced the coolest inferred temperatures of the Holocene.

3.4 pH

pH fluctuations seem to have been less pronounced at Lake Stora Kroksjön than at Lake Lilla Torkelsjön. In fact, there is not much evidence for pH changes in Lake Stora Kroksjön, and the diatom assemblage changes seem to be largely driven by the water-mixing regime in the late-glacial and by nutrient concentration in the Holocene. In Lake Lilla Torkelsjön, pH changes are registered and are considered to be partly connected with the water level changes and partly caused by anthropogenic impact on the lake catchment. It is surprising that a human-induced pH increase is not registered at Lake Stora Kroksjön, as settlement and land-use change took place beginning at the coast and moved northward (Björk et al., 1998), and thus should have reached Lake Stora Kroksjön first. Several possible explanations exist for why no pH change is observed. Either no pH increase has occurred, be it because the large water volume at Lake Stora Kroksjön was better buffered against imported agents, no slashing and burning took place within its catchment, or land-use activities only occurred to a small extent. A pH increase may have existed but the diatom response may have been overridden by other local environmental factors. Alternatively, the diatom reaction to the pH increase was simply not detected during analysis; however, no significant rates of change are registered around 2500 cal. yrs BP or later. It can be assumed that any pH change in Lake Stora Kroksjön was probably not so high as to affect the species community to a significant extent. In Lake Lilla Torkelsjön, however, pH may have fluctuated between 5.5 and circumneutral conditions. In both lakes, no signals of industrial acidification were found, though it is documented for both sites by the Blekinge Länstyrelsen. Probably, in both sites the uppermost sediment layers were not retrieved by the corer.

3.5 Anthropogenic disturbance

The vegetation records show the very first signs of alteration of the natural vegetation

around 5700 cal. yrs BP, when agriculture-related pollen types first become abundant. There are no records of pre-historic settlements in the vicinity of the study sites, and any permanent settlement was probably located much closer to the coast. However, the area may have been used in extensively for wood coppicing, creating open areas where meadow and pasture vegetation became established at least temporarily. Signs of slash-and-burn farming in the catchment of Lake Lilla Torkelsjön are dated to ca. 2600 cal. yrs BP, but were not detectable at Lake Stora Kroksjön. The most unmistakable sign of human impact in the lake catchment is the massive spread of beech forest starting around 2000 cal. yrs BP, the seeds of which need topsoil disturbance. The impact is strong on the profundal chironomid assemblage of Lake Stora Kroksjön and a similar, though weaker response of *Sergentia* is seen at Lake Lilla Torkelsjön.

Historic maps of the surroundings of Lake Lilla Torkelsjön mark only few settlements in the area at the beginning of the 19th century (Westerberg, 1814, cited in Bernhard, 1998), though increasing population density led to cultivation attempts even in the more remote and inaccessible areas of Blekinge (Björk et al., 1998). Some building ruins in the vicinity of Lake Lilla Torkelsjön from the end of the 19th century witness this attempt. No signal of alterations in the lake ecosystems can easily be linked with these colonisation attempts. Similarly, the impact of air-borne industrial pollution causing severe acidification is documented by the biota in neither of the study sites due to the reasons discussed earlier.

3.6 Sea-level changes

Even though Lake Stora Kroksjön had been part of the Baltic Ice Lake for a short period after the region emerged from under the ice sheet, any bearing upon the further development of the lake are not easy to discern from general ecological trends. In the sediments deposited during the BIL phase, fossil remains of the investigated biota were sparse and drew the picture of a hostile environment. It was only after the disconnection that a differentiated colonisation with midges and diatoms began.

The most obvious effect is the presence of the relict crustaceans *Mysis relicta*, *Monoporeia affinis* and *Pallasea quadrispinosa* in the system, which may have structured the food web of the lake in a specific way by their foraging activity. However, it is impossible to get an idea of the strength of such impact on the lake ecosystem over time without comparing it with a lake of similar morphology and physical and chemical background just above the highest coast line. Thus, a comparison with the shallow Lake Lilla Torkelsjön tells us little about lingering impacts of the BIL upon the species assemblages of Lake Stora Kroksjön. However, lakes lying at lower elevations and having become inundated by the brackish waters of the Littorina transgression may provide clearer signals within the chironomid and diatom fauna than Lake Stora Kroksjön (e.g., Hofmann and Winn, 2000, Yu et al., 2003 and Heinrichs and Walker, submitted).

4 Conclusions

During the last 14,000 years, the study area has changed considerably towards the present: From barren terrain in the lateglacial that emerged from the Baltic Ice Lake or directly from under the retreating ice sheet, soils and vegetation developed and affected the physical, chemical, biological and hydrological parameters of the regional lakes. Processes were, though more

ore less directly climate-related, not exclusively driven by temperature but were a result of the complex interactions and feedback mechanisms of the many biotic and abiotic factors structuring any ecosystem. Chironomids and diatoms responded to temperature, lake trophic status, change in catchment vegetation, pH changes and hydrology. Such, the application of within-lake biota as qualitative and quantitative indicators for environmental change has illustrated how local circumstances may override some regional and global signals, while they reflect others.

The results of this study underline that paleoecological interpretations based on single-proxy and/or single-site evidence may be compromised by the fact that environmental change through time is rarely a monocausal process. However, only few factors have ultimate control on ecosystems, and a careful choice of complementary proxies may provide a sophisticated picture of the processes active at different temporal and spatial scales. For example, the diatom water-depth preference was more significant than the temperature changes indicated by the midge fauna, and the multi-proxy approach allowed for a probably more correct interpretation of the variables driving the chironomid assemblage change. This is exemplary for Birks' (1990; 1995) statement that any environmental reconstruction may be compromised if the indicator organism is also responding to environmental or biological variables that are not linearly correlated to the reconstructed variable. The results confirm that chironomid-inferred temperature reconstructions based on single-core evidence need to be interpreted with caution (Velle, 2004), if temperature cannot be identified as the most important variable over the investigated time span and no complementary data is available.

The aims of this study, to 'describe the limnological, hydrological and ecological development of the study sites and to discern local effects at the individual study sites from temperature and environmental trends acting on a higher spatial scale', could have been reached even more effectively if transect cores had been used according to Digerfeldt (1988; 1998). In addition to giving evidence for recent acidification trends by documenting the most recent changes in the lake species communities, specifically at Lake Lilla Torkelsjön, this may have contributed to the evidence for lake-level change. As the shallow parts of Lake Lilla Torkelsjön seem to have been dry land for many hundred years, inundated soils and plant remains are likely to be found under the Subatlantic sediments.

The absolute outcome of the mean July air temperature reconstruction has been influenced by the depth of the chosen lakes. It seems that in lakes with a well-developed profundal chironomid community, absolute temperatures tend to be underestimated. In future studies including chironomids as quantitative temperature indicators, lakes with intermediate water depth, i.e. that do not become thermally stratified, should be chosen to overcome the impact of a profundal chironomid assemblage on the absolute outcome of the temperature reconstruction.

The study of subfossil assemblages does not reveal biotic interactions, be it on intra- or interspecific level. Any interspecific interaction, predation and concurrence effects are already incorporated in the fossil signal. To discern such biotic interaction from environmental effects, a profound knowledge about species' autecology and distribution is needed and may contribute to more appropriate interpretation of species assemblage change in the past. Thus, the knowledge and intuition of the ecologist cannot be entirely replaced by statistical treatment of paleoenvironmental data.

It is evident that paleolimnology may greatly contribute to the efforts of restoration and conservation of freshwater ecosystems, which is one of the most important and challenging economic and scientific issues of the coming century. Reconstructing ecosystem baseline data prior to human impact may help to develop and formulate realistic aims in ecosystem management (Smol, 1992). Reconstructing and quantifying past trophic lake status and understanding the mechanisms governing eutrophication processes and its impacts on lake and river ecosystems and their species communities may eventually become an even more important issue in paleolimnological research than it is today.

Chapter VII

Annex

Chironomid Taxa List with some notes on taxonomy

Prodiamesinae and Diamesinae
Monodiamesa
Procladius

Tanypodinae
Ablabesmyia: specimens of the genus Ablabesmyia were identified by the setational arrangement using Rieradevall and Brooks (2001). Ventral setal arrangement differed somewhat from the literature, due to the fact that nearly all specimens were third instar head capsules.
Conchapelopia
Guttipelopia
Krenopelopia
Paramerina
Pentaneurini: All Tanypodinae with bifid paraligula that could not be determined closer.
Procladius
Tanypodinae: All Tanypodinae which could not be determined more specifically, most often due to loss of even ligula and paraligula and bad preparation.

Orthocladiinae
Acamptocladius
Corynoneura/Thienemanniella: These genera can in subfossil material only be separated by the number of segments of the antenna, which are lost in almost all cases. *Corynoneura* has 4 segments, *Thienemanniella* 5. *Corynoneura scutellata*, however, shows a distinct pattern of sculpturing marks on the dorsal surface of the head capsule.
Cricotopus: Comprises all Cricotopus that were not be further separated.
Cricotopus cylindracaeus
Cricotopus tremulus
Heterotrissocladius grimshawi
Heterotrissocladius maeaeri
Heterotanytarsus
Hydrobaenus
Limnophyes
Mesocricotopus
Mesopsectrocladius
Metriocnemus
Nanocladius
Orthocladiinae indet. In this category all specimens were placed, which could, by the number of teeth and by the lack of distinct, striated submental plates, readily be identified as Orthocladiinae, but no further determination was possible. Mostly this occurred when preparation was bad or with some early instars.
Parakiefferiella bathophila
Parakiefferiella fennica
Psectrocladius septentrionalis: comprises the head capsules described in Wiederholm (1983, p. 268) as *Monopsectrocladius* sp. nr. *calcaratus* Edwards (Fig. 9.61C) and *Psectrocladius septentrionalis* (Chernovski).
Psectrocladius sordidellus-group
Pseudorthocladius
Rheocricotopus
Synorthocladius
Synorthocladius
Tvetenia
Zalutschia

Chironomini

Chironomini larvula: Under this term falls a uniform morphology: one median tooth, 6 lateral teeth, submental plates triangular with the upper margin serrate. These specimens are thought to be an early instar of a otherwise known genus, but can so far not be assigned to a taxon. This hypotheses is, on the other hand, hard to hold against the background of the distinct boundaries of occurrence within the stratigraphies.

Chironomus anthracinus-gr. sensu Hofmann (1971b). Probably these features (second last lateral tooth bigger than third last; mandibles with two inner teeth) apply for more than one species.

Chironomus plumosus-gr. sensu Hofmann (1971b). Probably these features (second last lateral tooth smaller than third last; mandibles with three inner teeth) apply for more than one species.

Cryptochironomus

Cladopelma lateralis

Demicryptochironomus

Dicrotendipes

Dicrotendipes pulsus

Einfeldia

Endochironomus albipennis

Glyptotendipes pallens

Lauterborniella agrayloides

Microtendipes pedellus

Nilothauma

Omisus

Pagastiella orophila

Parachironomus

Paracladopelma

Paratendipes

Phaenopsectra: specimens of the genus Phaenopsectra were assigned to species *P. flavipes* in Lake Stora Kroksjön by comparison with drawings in Wiederholm (1983). In Lake Lilla Torkelsjön however, specimens could not be identified to species level. They were distinguished from the genera *Sergentia, Stictochironomus, Endochironomus* and *Tribelos*, who all have a comparable pattern of mental tooth arrangement, by the combination of the following characters: Antennae 5-segmented (6-segmented in *Stictochironomus*), mandibles with 3 inner teeth (4 inner teeth in *Sergentia*), dorsal tooth short, not standing out beyond apical tooth as in *Stictochironomus*, trifid premandibels (bifid in *Tribelos*), pecten epipharingys with smooth surface (surface teeth in *Endochironomus* and *Tribelos*), seta mandibularis simple (distally divided in *Endochironomus*), frontal apotome convex, only labral sclerite 2 present (1 and 2 present in *Tribelos*) and S1 and S2 not triangular (triangular in *Endochironomus*).

Polypedilum convictum

Polypedilum nubeculosum

Polypedilum pedestre

Pseudochironomus

Sergentia coracina

Stempellina

Stempellinella

Stenochironomus

Stictochironomus

Tribelos

Zavrelia

Tanytarsini

Cladotanytarsus mancus-gr.

Corynocera ambigua

Micropsectra insignilobus-gr.

Paratanytarsus

Tanytarsini: All Tanytarsini lacking further identification characteristics.

Tanytarsus sp-gr. B: Tanytarsus with the combination of the following characters were assigned to species group B: pedestal broad, without spur. Mandibles: Three inner teeth, one dorsal tooth.

Tanytarsus sp-gr. C

Tanytarsus chinyensis

Tanytarsus lugens type

Tanytarsus pallidicornis-gr.: Tanytarsus with the combination of the following characters were assigned to subspecies group pallidicornis: Mandibles with 2 inner teeth, a third sometimes vestigial, one dorsal tooth. Pedestal with broad, blunt spur.

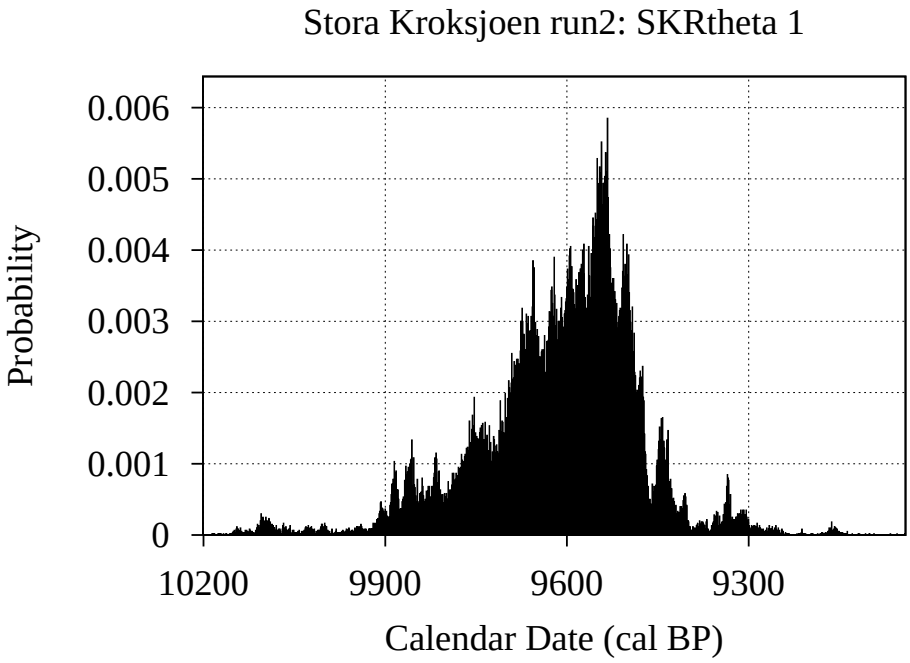


Figure VII.1: Posterior Probability density plot of Stora Kroksjön 237.5-240 cm. Graph is generated by the software BCal (Buck et al., 1999).

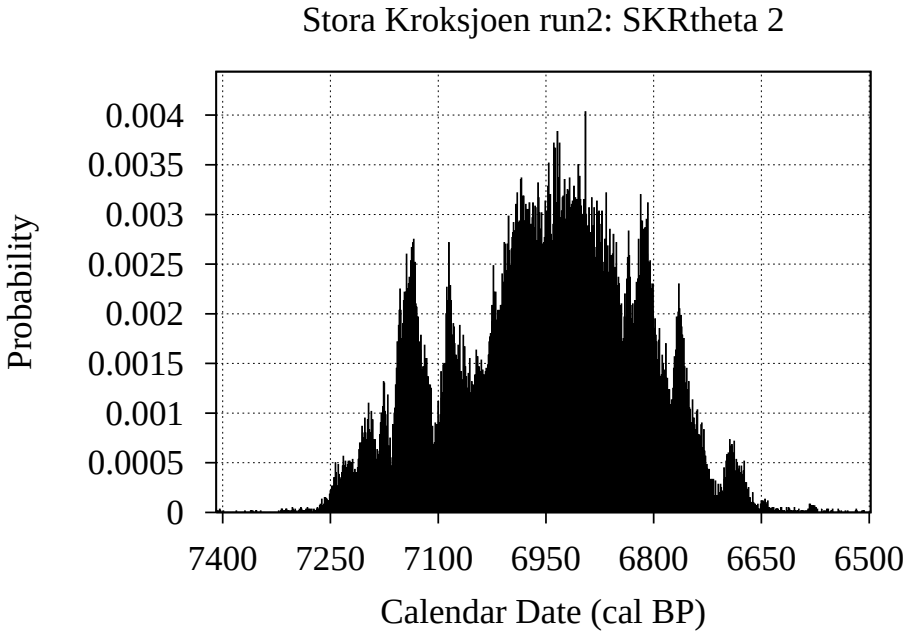


Figure VII.2: Posterior Probability density plot of Stora Kroksjön 187.5-190 cm. Graph is generated by the software BCal (Buck et al., 1999).

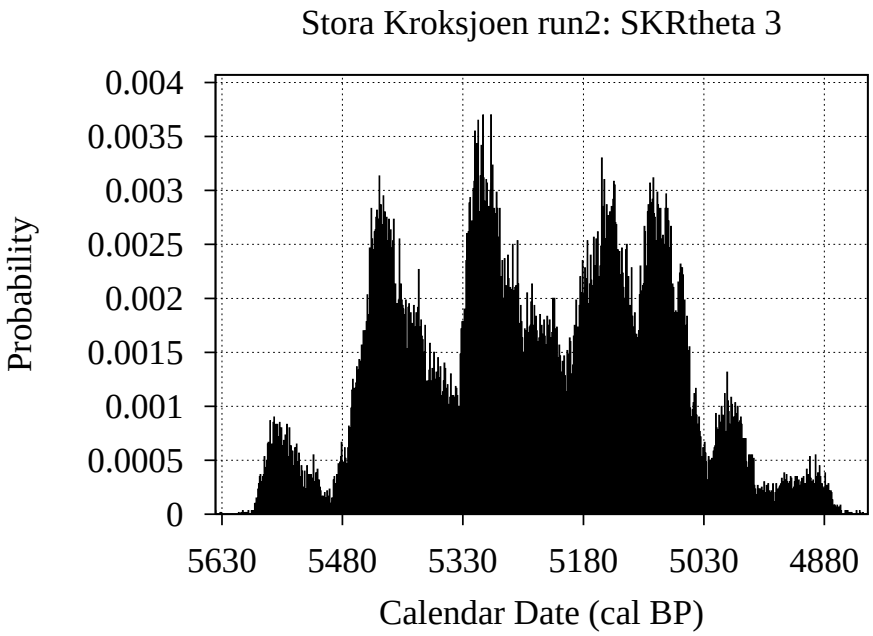


Figure VII.3: Posterior Probability density plot of Stora Kroksjön 137.5-140 cm. Graph is generated by the software BCal (Buck et al., 1999).

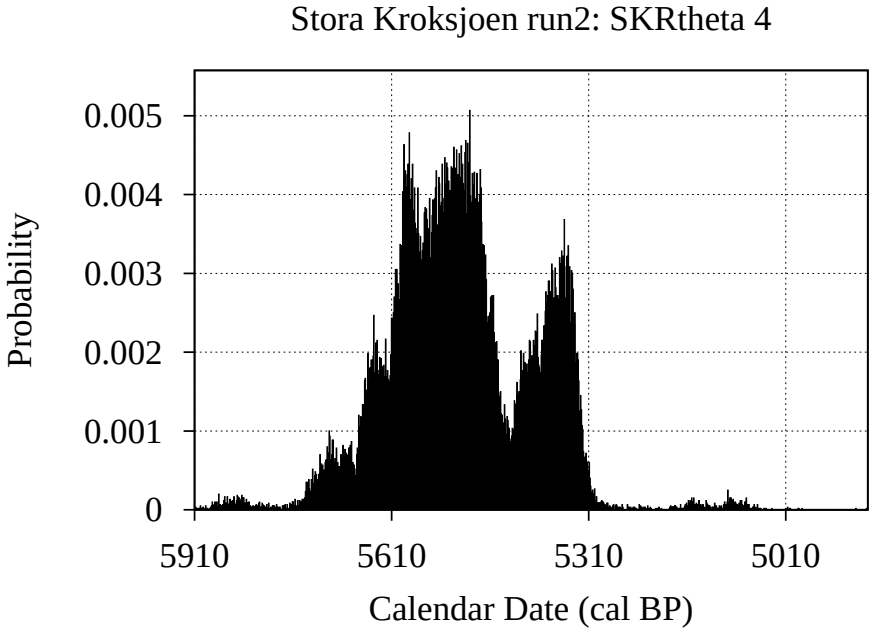


Figure VII.4: Posterior Probability density plot of Stora Kroksjön 142.5-145 cm. Graph is generated by the software BCal (Buck et al., 1999).

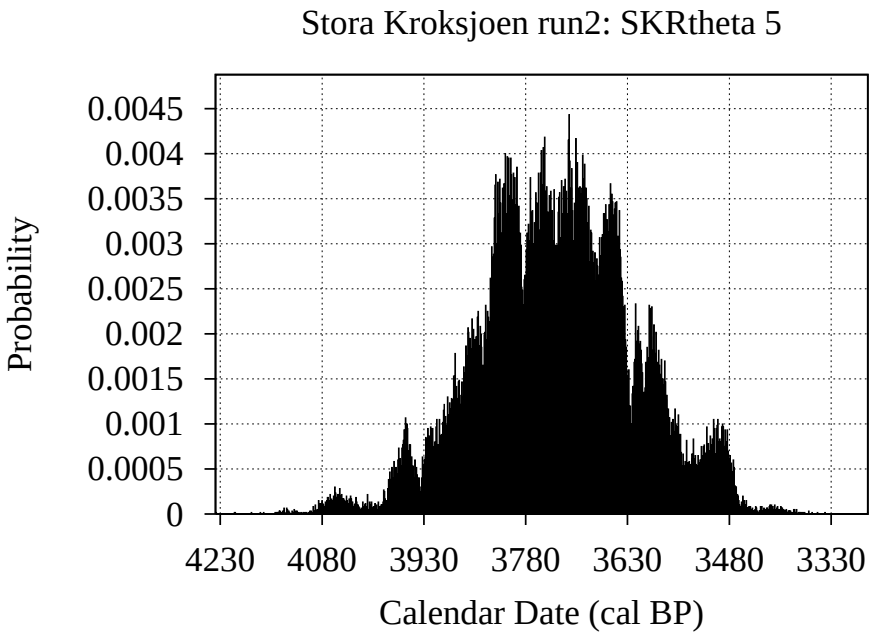


Figure VII.5: Posterior Probability density plot of Stora Kroksjön 97.5-100 cm. Graph is generated by the software BCal (Buck et al., 1999).

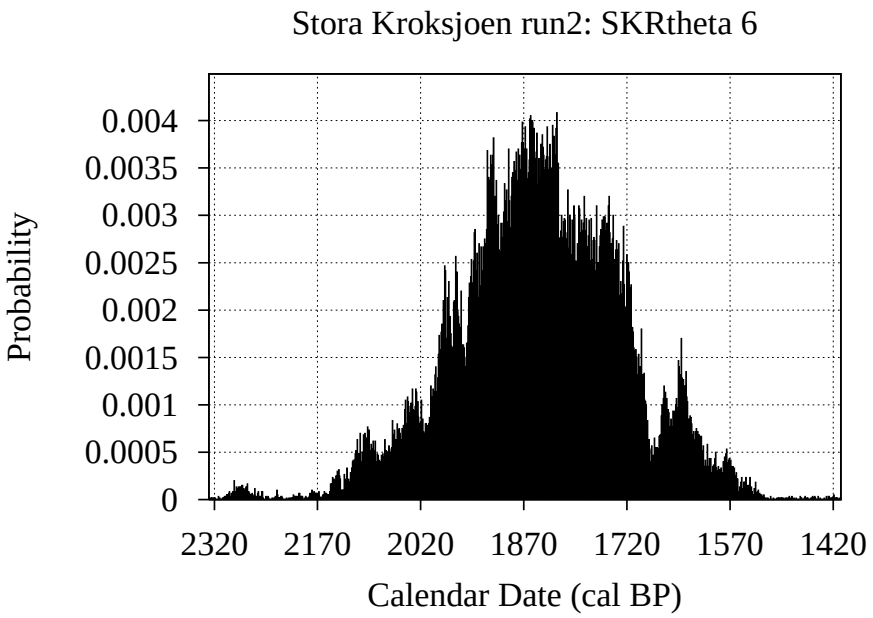


Figure VII.6: Posterior Probability density plot of Stora Kroksjön 47.5-50 cm. Graph is generated by the software BCal (Buck et al., 1999).

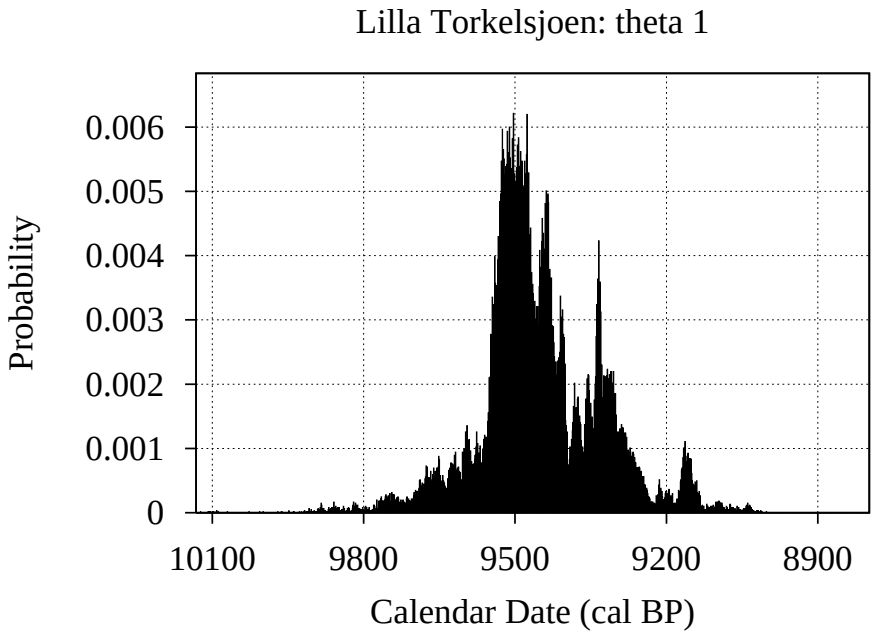


Figure VII.7: Posterior Probability density plot of Lilla Torkelsjön 307.5-310 cm. Graph is generated by the software BCal (Buck et al., 1999).

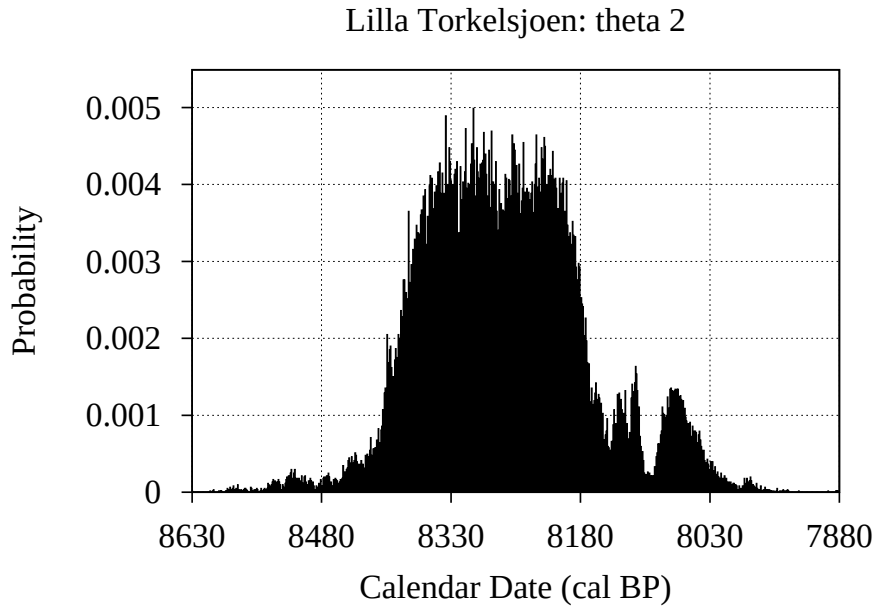


Figure VII.8: Posterior Probability density plot of Lilla Torkelsjön 247.5-250 cm. Graph is generated by the software BCal (Buck et al., 1999).

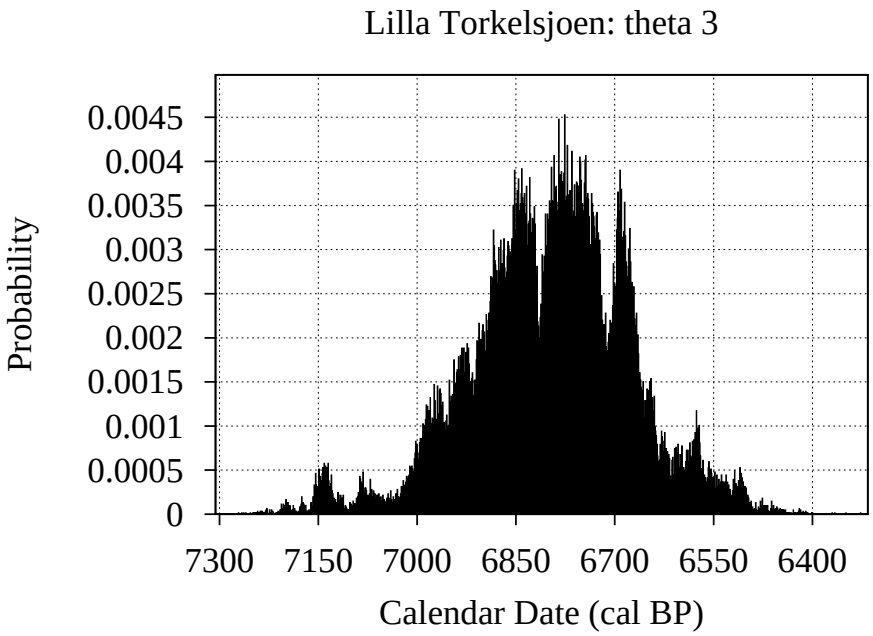


Figure VII.9: Posterior Probability density plot of Lilla Torkelsjön 197.5-200 cm. Graph is generated by the software BCal (Buck et al., 1999).

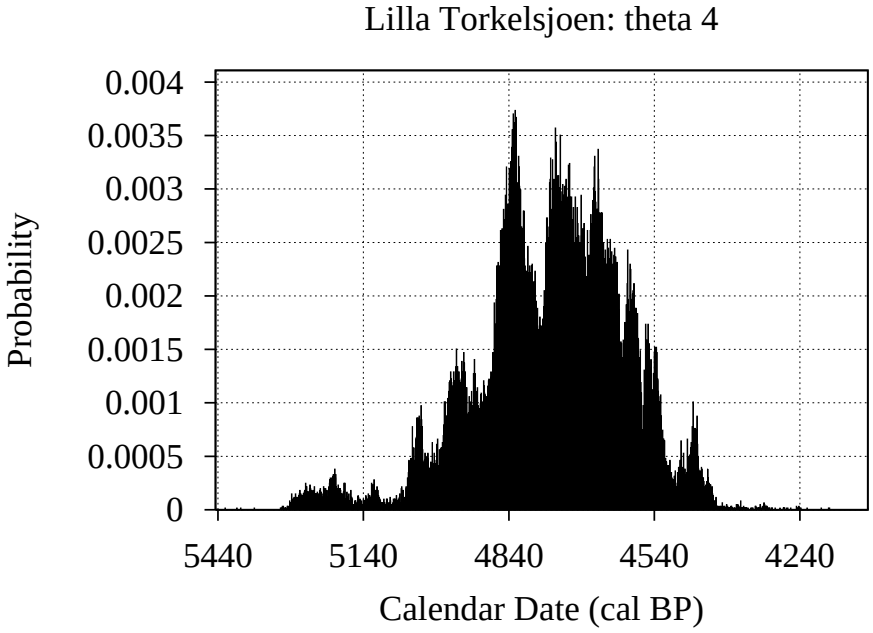


Figure VII.10: Posterior Probability density plot of Lilla Torkelsjön 147.5-150 cm. Graph is generated by the software BCal (Buck et al., 1999).

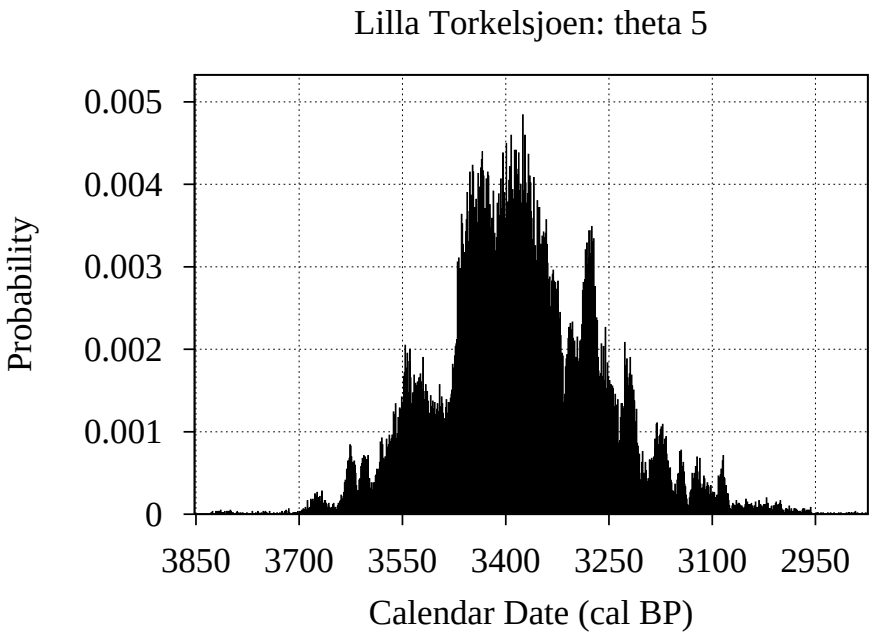


Figure VII.11: Posterior Probability density plot of Lilla Torkelsjön 97.5-100 cm. Graph is generated by the software BCal (Buck et al., 1999).

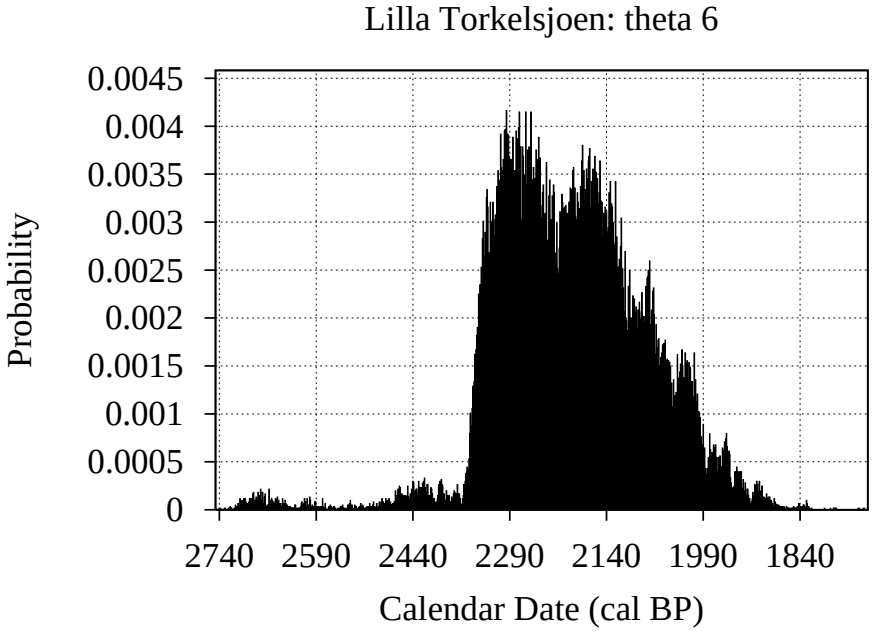


Figure VII.12: Posterior Probability density plot of Lilla Torkelsjön 47.5-50 cm. Graph is generated by the software BCal (Buck et al., 1999).

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